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BOOK REVIEW

ANNOUNCEMENT

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SEED RAIN DURING EARLY PRIMARY SUCCESSION, MOUNT ST. HELENS, WASHINGTON

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ABSTRACT

Seed rain into sites undergoing primary succession on Mount St. Helens was measured from 1982 to 1986 and again from 1989 to 1990. Study sites were devastated in 1980 by pyroclastic flows of pumice, searing blasts, and lahars. Most sites were several km or more from seed sources. Seed rain density averaged 34 seeds 0.1 m^{-2} yr^{-1} in mid-elevation barren sites, 1083 seeds 0.1 m^{-2} yr^{-1} in mid-elevation vegetated sites and 2 seeds 0.1 m^{-2} yr^{-1} at subalpine barren sites. A total of 33 species was collected in traps. The relative abundance distributions of species were generally similar across years and sites. A few wind-dispersed species accounted for most of the seed rain: *Anaphalis margaritacea* (L.) Benth. & Hook., *Epilobium angustifolium* L., *E. watsonii* Barbey (*E. ciliatum* Raf.), *Hieracium albiflorum* Hook., and *Hypochaeris radicata* L. Seeds of trees and shrubs were virtually absent. The common species in the seed rain were also the most common species in the vegetation, although their absolute abundance is determined by environmental factors. Many uncommon species occurred in the vegetation that were not recorded in the seed rain. Two taxa common in the vegetation, *Lupinus lepidus* Douglas and *Salix* spp., were rare in the seed rain. For *Salix,* this is because seed dispersal occurred before traps were in place for the season. *Lupinus lepidus* is not wind dispersed and seeds are not likely to enter traps. We conclude that the seed rain on Mount St. Helens is apparently sufficient to initiate colonization but is depauperate in species. At present the vegetation generally reflects the incoming seed rain.

One cause of succession is differential species availability at a site after a disturbance (Pickett et al. 1987). For vascular plants this differential availability occurs mostly by vegetative regrowth, seed banks, or seed dispersal. In primary succession colonization results mainly from seed dispersal. On large scale primary successional landscapes the input or "rain" of seeds from long-distance dispersal is the main source for the establishment of most species, because seed banks and regrowth are absent. A complete interpretation of primary succession in particular, and community assembly in general, must therefore include measurements of the density and species composition of the seed rain along with an assessment of environmental and substrate conditions (Wood and del Moral 1987; del Moral 1993; Chapin et al. 1994; Booth and Larson 1998; Dlugosch and del Moral 1999). For example, the absence of a species from a particular site or seral stage could be due as much to its absence from the seed rain as to its inability to establish. Conversely, high abundance of a colonist may be explained as much by its abundant seed rain as by its environmental tolerance, growth rate, or competitive ability. Hypothesized mechanisms of succession such as facilitation (Connell and Slatyer 1977; Morris and Wood 1989) must also consider differential species availability through the seed rain.

Studies of seed dispersal generally are of two types: studies of individual species with the parent plant and its seed shadow as the focus (reviews in Harper 1977; Willson 1993), or studies of the long-distance seed rain into sites where specific seed sources cannot be identified precisely. Seed rain measurements are most appropriate for studies of community assembly in primary succession, but published studies are few (Ryvarden 1971; Stöcklin and Bäumler 1996; Archibold 1980; Jefferson and Usher 1989; Chapin et al. 1994). This paper describes the density and species composition of the seed rain in several contrasting regions and habitats undergoing primary succession on Mount St. Helens, WA.

The rate of vegetation recovery and plant species composition at various sites have been described for Mount St. Helens following the catastrophic eruption in 1980 (del Moral 1983; Wood and del Moral 1987; del Moral and Wood 1988; del Moral 1993; del Moral and Bliss 1993; del Moral and Wood 1993a, b; del Moral et al. 1995; del Moral 1998, del Moral 1999), but detailed species seed rain data have not been reported with the exception of Dale (1989) who sampled lower elevation lahar (mudflow) sites not included in this study. We pose these questions: For a given site, what is the density and species composition of the seed rain? How do islands of established, reproducing vegetation affect
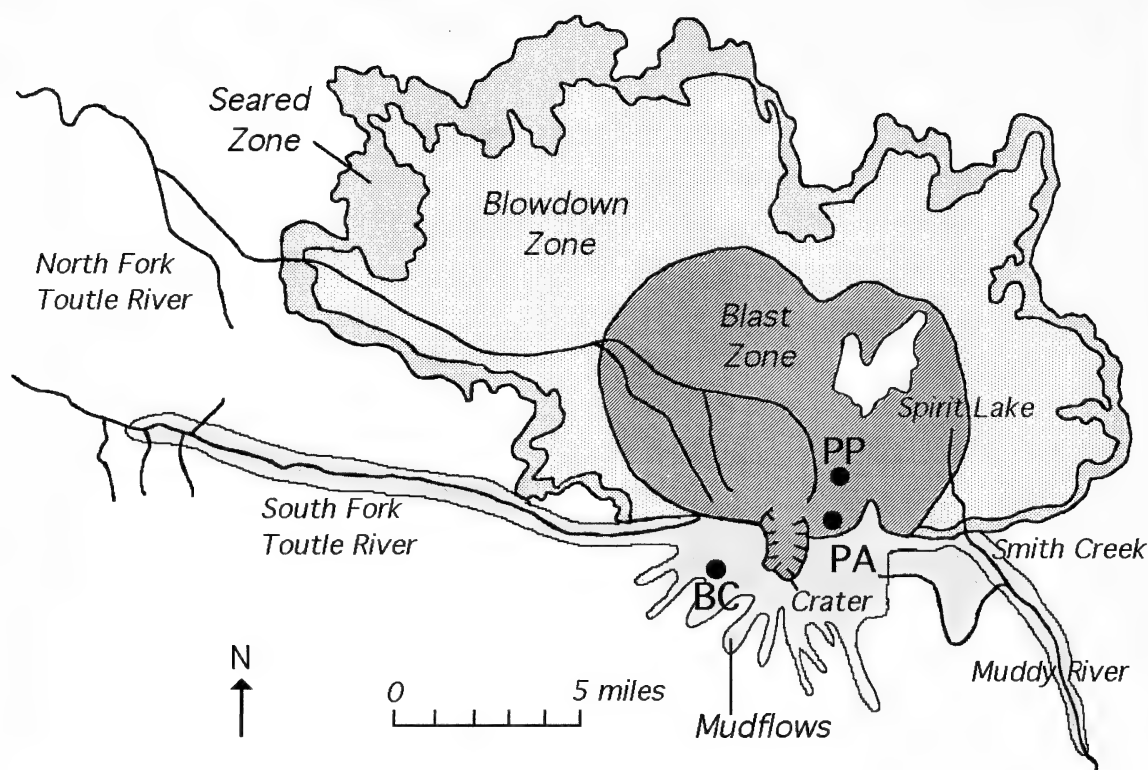
Fig. 1.   Location of study areas. PP = Pumice Plain sites, PA = Plains of Abraham sites, BC = Butte Camp sites. See text for details of seared, blowdown, and blast zones.

the local seed rain? Does the species composition of the seed rain reflect the species composition of the colonizing flora? Are there species present in the seed rain but absent as colonists? Are there species present as colonists but absent from the seed rain?

STUDY AREA

The Mount St. Helens volcano is in the Cascade Range of southwestern Washington at 46°12′N, 122°11′W. The catastrophic north-directed eruption of May 18, 1980, produced a variety of impacts including: a debris avalanche; pyroclastic flows, or incandescent flows of gas and pumice; and lahars, flows of water-saturated debris ("mudflows") triggered by rapidly melting snow and ice (Lipman and Mullineaux 1981; Decker and Decker 1981). Impacts on the vegetation are categorized into four regions: the blast zone, in which most life was destroyed; the blowdown zone, in which adult trees were knocked over but some saplings and understory vegetation survived; the seared zone, in which trees remained standing but had their foliage singed by the hot gases of the blast, and the mudflow (lahar) zone in which most vegetation was destroyed (Fig. 1). In addition to these four regions, a large region south of the crater received 5–20 cm

of tephra (airfall ash and pumice) and most vegetation survived.

We studied three main areas separated by several km and at different elevations: Pumice Plain, Plains of Abraham (both in the blast zone), and Butte Camp (Fig. 1). The Pumice Plain is a 20 km² region between the crater and Spirit Lake that received the full force of the north-directed lateral eruption, receiving a debris avalanche and pyroclastic flows. These new deposits now overlie what was formerly a montane forest of *Tsuga heterophylla* (Raf.) Sarg., *Pseudotsuga menziesii* (Mirbel) Franco, and *Abies amabilis* (Douglas) James Forbes (Kruckeberg 1987). Elevations range from 1000 to 1200 m. Although much of the Pumice Plain was initially flat to moderately hilly, numerous erosion gullies continue to form and deepen. The Plains of Abraham, also a pumice landscape, is located approximately 3 km NE of the crater at 1350 m elevation. It received searing blasts and deposits of tephra, and is predominantly flat with numerous small gullies (del Moral and Wood 1993b). The pre-eruption vegetation of this high montane region was described by Kruckeberg (1987) as a region high in species richness of forbs and grasses but low in cover with scattered conifers. The Butte Camp region is located on the southwest side of the volcano

TABLE 1. MEAN ± STANDARD ERROR OF SEED RAIN DENSITY (SEEDS 0.1 M^{-2} YR^{-1}) FOR 1983 TO 1986 ESTIMATED FROM FALLOUT TRAPS AT MID-ELEVATION BARREN SITES. Number in parentheses is number of traps. In 1983 and 1984, mean values for the Pumice Pond and Spirit Lake sites are significantly different.

Pumice Plain Sites	1983	1984	1985	1986
Pumice Pond	75.5 ± 9.5 (10)	38.4 ± 9.6 (5)	no data	no data
Spirit Lake	34.9 ± 5.0 (10)	13.0 ± .9 (9)	25.02 ± 3.0 (10)	26.9 ± 4.9 (10)

at 1500 to 1600 m. This area of subalpine vegetation was disturbed by several lahars and also received tephra deposits (del Moral 1983; del Moral and Wood 1986). However, seed rain was only measured at the primary succession lahar sites.

METHODS

Seed collections. Seeds of vascular plants were collected from both wet pitfall traps and dry fallout traps. Pitfall traps, whose primary purpose was to collect ground-dwelling insects (Edwards 1986), consisted of 10 cm diameter plastic cups filled with ethylene glycol, set flush with the ground surface, and covered by a plywood square elevated 1 cm above the cup with corner nails. Pitfall trap data were collected in 1982, 1983 and 1985. The fallout traps consisted of 33 × 33 cm (0.1 m^2) wooden frames 3 cm high with fine nylon mesh bottoms. Frames were filled with a single layer of used golf balls and set flush with the surface (Edwards 1986; Edwards and Sugg 1993). The golf balls (approximately 3 cm in diameter) were used because they were an easily obtainable uniform sphere that mimicked the size and surface texture of the pumice. We also wanted baseline density estimates of the seed rain for relatively flat, open ground. These baseline values may then be adjusted upwards if desired for sites of seed accumulation, e.g., against boulders or in gullies and other depressions (Dale 1989). Sticky traps (Werner 1975) or wet pitfall traps could yield over-estimates of density for flat ground in this open, windy environment due to seed accumulation (Johnson and West 1988). Thus, only fallout traps were used to estimate seed rain density. Fallout traps were used in all years of the study except 1982, and were the only type of trap used in 1989 and 1990. Data from both pitfall traps and fallout traps were used to estimate relative abundance.

Traps were set out in June of each year after snowmelt when the roads to the sites became accessible and contents were collected approximately twice a month until November. Fallout traps were collected only once a year in late October, after the fall dispersal period and before sites became inaccessible due to snow. Seeds were stored in alcohol or formalin-acetic acid-alcohol (FAA) and were identified using a reference collection obtained from field specimens and herbarium sheets. Although seed germination was not measured in this study, only those seeds with morphology and coloration similar to viable seeds were counted. Extensive seed germination experience with many species from Mount St. Helens suggests that the appearance of viability under a dissecting microscope is a good predictor of germination—most species had germination rates from 60 to 90% when abnormal-appearing seeds were excluded (Wood and del Moral 1987; Wood unpublished data). Nomenclature follows Hitchcock and Cronquist (1973) with parenthetical updates from Hickman (1993) to correspond to Titus et al. (1998).

Study sites. From 1982 to 1986 two sites on the Pumice Plain were sampled, Pumice Pond and Spirit Lake. The Pumice Pond site was near the headwaters of the North Fork of the Toutle River on the northwest side of the Pumice Plain about 5 km NNW of the crater. Unfortunately, severe erosion at this site forced it to be abandoned in 1985 (Edwards and Sugg 1993). The Spirit Lake site was near the eastern edge of the Pumice Plain about 2 km south of Spirit Lake and 3 km north of the crater. Traps of both types (pitfall and fallout) were placed at 10 m intervals along 100 m transects, although resultant sample sizes vary because traps occasionally were filled with erosional material or lost (Tables 1 and 3). In 1986 mean percent cover of vegetation on the Pumice Plain in the vicinity of these sites was estimated at 0.09% (Wood and del Moral 1988) and had increased to only 1.4% by 1990 although some small patches exceeded 50% (Wood unpublished data).

In 1989 and 1990, the number and placement of fallout traps was increased by including a greater variety of habitats within the Pumice Plain. Pumice Plain sites I and II were established in barren areas (defined as having <3% cover) close to the old Spirit Lake site at 1100 m elevation. Each site contained 16 fallout traps arranged in a 4 × 4 grid with traps separated by 10 m (hereafter referred to as a "16-FT grid"). Due to occasional trap disturbance (e.g., by ravens and elk) resultant sample size again varied (Table 2). The Pumice Ridge site was on an exposed, barren ridge 50 m above the Pumice Plain and contained 5 traps along a 30 m transect. The 16-FT grid Lupine Patch site was in a patch of dense flowering *Lupinus lepidus* Douglas, (>50% cover) a few hundred m from Pumice Plain I and II. The Willow Spring 16-FT grid was in a relatively open, moderately vegetated site (<20% cover) but was surrounded by a stand of dense, reproductively mature vegetation adjacent to a spring (Wood and del Moral 1988). This vegetation included *Salix* spp. (primarily *S. sitchensis* Bong. and

TABLE 2. MEAN ± STANDARD ERROR OF SEED RAIN DENSITY (SEEDS 0.1 M^{-2} YR^{-1}) IN 1989 AND 1990. Number in parentheses is number of traps. Means with the same letter within a year are not significantly different at P = 0.05 by Tukey's HSD. MEB = mid-elevation barren; MEV = mid-elevation vegetated; HEB = high-elevation barren.

	Habitat	1989	1990
Butte Camp Sites			
Lahar I	HEB	1.2^a ± 0.7 (15)	no data
Lahar II	HEB	2.8^a ± 0.8 (16)	no data
Plains of Abraham Sites			
Abraham I	MEB	11.8^b ± 1.7 (16)	5.3^a ± 2.8 (16)
Abraham II	MEB	9.0^b ± 2.0 (5)	66.5^{a,b} ± 12.3 (4)
Pumice Plain Sites			
Pumice Plain I	MEB	24.7^{b,d} ± 4.1 (15)	50.6^a ± 8.2 (16)
Pumice Plain II	MEB	21.9^{b,d} ± 3.3 (15)	50.6^a ± 8.2 (16)
Pumice Ridge	MEB	68.2^{c,d} ± 19.4 (5)	9.6^a ± 2.3 (5)
Lupine Patch	MEV	94.1^c ± 10.8 (16)	355.6^b ± 48.6 (16)
Willow Spring	MEV	1709.1 ± 489.7 (16)	2174.4 ± 645.1 (16)

S. commutata Bebb), *Anaphalis margaritacea* (L.) Benth. & Hook., *Epilobium angustifolium* L., *E. watsonii* Barbey (*E. ciliatum* Raf.), *Hypochaeris radicata* L., and *Lupinus lepidus*.

The Plains of Abraham area contained two sites in barren areas, one 16-FT grid (Abraham I) and one five-trap transect (Abraham II) similar to the Pumice Ridge site described above. Both sites were on nearly level ground and were spaced 200 m apart. In 1989 and 1990, mean percent cover on the Plains of Abraham was estimated at 0.12% and 0.23%, respectively (del Moral and Wood 1993b).

The Butte Camp area contained two sites on lahars (Lahar I and II), both 16-FT grids spaced 200 m apart. Percent cover on the Butte Camp lahars was estimated at 2–3% in 1989 (del Moral 1993).

RESULTS

Density. Seed rain density varied widely over both sites and years (Tables 1 and 2), from a low of 1.2 seeds 0.1 m^{-2} yr^{-1} at Lahar II in Butte Camp in 1989 to a high of 2174 seeds 0.1 m^{-2} yr^{-1} at Willow Spring on the Pumice Plain in 1990 (Table 2). In 1983 and 1984 the Pumice Pond site received

more than twice as many seeds as did the Spirit Lake site (Table 1; t-test, log transformation, P < 0.01 in each year). In both 1989 and 1990, ANOVA revealed a significant difference among the Pumice Plain, Plains of Abraham, and Butte Camp areas as well as significant differences among sites within the Pumice Plain (Table 2; log transformation, P < 0.001 in each year). In both 1989 and 1990, Willow Spring had a significantly greater seed rain density than all other sites (Table 2; Tukey's HSD multiple comparisons, P = 0.05). Lupine Patch had the second highest seed rain density in both years, although mean density at this site was not significantly different from Pumice Ridge in 1989 or Abraham II in 1990 (Table 2). Statistical tests were not performed on year-to-year differences within a site due to the lack of clear hypotheses, as variation could be due to unmeasured factors such as differences in wind patterns or growing conditions and seed production in surrounding landscapes.

When sites were classified by habitat, the variation in density was reduced and a clearer pattern emerged. Mid-elevation barren sites (Pumice Pond, Spirit Lake, Pumice Plain I and II, Pumice Ridge,

TABLE 3. RELATIVE ABUNDANCE OF COMMON SPECIES IN THE SEED RAIN FOR 1982 THROUGH 1986. The Pumice Pond and Spirit Lake sites are combined. See text for additional species. Distributions between years are not significantly different by a Wilcoxon Signed Ranks test.

	Relative Abundance (%)				
	1982	1983	1984	1985	1986
Anaphalis margaritacea	16	36	21	10	70
Epilobium angustifolium	26	8	48	74	13
Epilobium watsonii (*E. ciliatum*)	<1	5	10	3	5
Hypochaeris radicata	3	2	3	5	3
Hieracium albiflorum	3	2	3	1	3
Senecio sylvaticus	36	39	7	1	1
Lupinus lepidus	0	0	0	0	0
Number of pitfall traps	38	32	0	35	0
Number of fallout traps	0	20	14	10	10

Abraham I and II) had an overall mean density of 33.6 seeds 0.1 m^{-2} yr^{-1}, ranging from 5.3 at Abraham I in 1990 (Table 2) to 75.5 at Pumice Pond in 1983 (Table 1). High-elevation barren sites (Lahar I and II) had a much lower overall mean density of 1.9 seeds 0.1 m^{-2} yr^{-1}. The highest densities were recorded at mid-elevation vegetated sites (Lupine Patch and Willow Spring) where densities ranged from 94.1 at Lupine Patch in 1989 to 2174 at Willow Spring in 1990 (Table 2) with an overall mean density of 1083.

Relative abundance. The relative abundance of the most common species in the seed rain is presented in Tables 3 and 4. Relative abundance distributions were generally consistent from year to year and from site to site. The most distinctive sites were Lahar I and II, where subalpine species characteristic of that habitat appear. However, no comparison of abundance distributions is significantly different, either among years from 1982 to 1986 (Table 3), between years within a site, or among sites in 1989 and 1990 (Table 4; Wilcoxon Signed Rank Test, all P > 0.5). Unfortunately, separate estimates of relative abundance for the Pumice Pond and Spirit Lake sites are not available because sample collections from these sites were combined after counting the total number of seeds in a given trap.

Six species accounted for 85% of the measured seed rain at the two Pumice Plain sites in 1982 and >90% from 1983 to 1986: *Anaphalis margaritacea, Epilobium angustifolium, E. watsonii (E. ciliatum), Hypochaeris radicata, Hieracium albiflorum* Hook., and *Senecio sylvaticus* L. (Table 3). Six species also accounted for >90% of the measured seed rain at all sites in 1989 and 1990 except for the subalpine sites Lahar I and II (Table 4). These were the same six species listed above except that *Lupinus lepidus* replaced *S. sylvaticus*. The decline of *S. sylvaticus* and the increase of *L. lepidus* were the most noteworthy changes in relative abundance during this study. *S. sylvaticus* decreased from 39% relative abundance in 1983 to zero in 1989 and 1990 at all sites except Lahar I and II (Tables 3 and 4). *Lupinus lepidus* was not recorded from 1982 to 1986 but during the 1989–1990 sampling period it occurred at all sites except Abraham II at least once.

A total of 33 species was collected, including two unidentified grasses (one seed each). Species not listed in Tables 3 or 4, all with three or fewer seeds trapped except as noted, are: *Acer circinatum* Pursh, *Achillea millefolium* L., *Agoseris grandiflora* (Nutt.) E. Greene, *Agrostis* sp., *Antennaria* sp., *Carex mertensii* Prescott, *Carex rossii* Boott, *Carex* sp., *Cinna latifolid* (Goeppert) griseb., *Cirsium vulgare* (Savio) Ten., *Epilobium luteum* Pursh, *Juncus parryi* Engelm., *Lactuca muralis* (L.), Fresen. *Penstemon cardwellii* Howell, *Salix* spp. (12 seeds), *Saxifraga ferruginea* Graham, *Senecio vulgaris* L., *Sitanion hystrix* (Nutt.) J. G. Smith (*Elymus ely-*

TABLE 4. RELATIVE ABUNDANCE OF COMMON SPECIES IN THE SEED RAIN FOR 1989 AND 1990. See text for additional species. All values are %. Distributions between years within a site or among sites are not significantly different by a Wilcoxon Signed Ranks test.

	Pumice Plains I '89	Pumice Plains I '90	Pumice Plains II '89	Pumice Plains II '90	Pumice Ridge '89	Pumice Ridge '90	Lupine Patch '89	Lupine Patch '90	Willow Spring '89	Willow Spring '90	Plains of Abraham I '89	Plains of Abraham I '90	Plains of Abraham II '89	Plains of Abraham II '90	Lahar I '89	Lahar II '89
Anaphalis margaritacea	29	24	42	47	40	17	18	22	4	4	6	15	11	17	0	0
Epilobium angustifolium	26	54	40	39	18	13	6	6	1	4	67	69	20	13	22	18
Epilobium watsonii	19	5	5	4	12	0	36	30	95	89	9	5	2	0	0	0
Hypochaeris radicata	14	11	7	3	13	58	8	29	<1	1	11	3	38	58	17	5
Hieracium albiflorum	2	4	2	3	2	10	1	4	<1	<1	1	1	2	10	6	5
Lupinus lepidus	<1	0	0	1	13	0	29	8	<1	<1	0	1	0	0	33	2
Senecio sylvaticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1
Cirsium arvense	0	<1	0	<1	0	0	0	<1	0	0	0	0	0	0	0	0
Spraguea umbellata	0	0	0	0	0	0	0	<1	0	0	0	0	0	0	6	27
Polygonum newberryi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27
Aster ledophyllus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	7
Lomatium martindalei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0
Hieracium gracile	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7

moides (Raf.) Swezey), *Sonchus asper* (L.) Hill, and *Taraxacum officinale* Wigg.

As with density, a classification of sites by habitat resulted in a clearer pattern of relative abundance. In both the mid-elevation barren sites and Lupine Patch (which had vegetation mostly <15 cm in height), *Anaphalis margaritacea* and *Epilobium angustifolium* dominated the seed rain. At Willow Spring, which had taller surrounding vegetation (up to 2 m) including a vigorous flowering population of *E. watsonii* (*E. ciliatum*), seeds of *E. watsonii* were dominant. Still, densities of *A. margaritacea* and *E. angustifolium* at Willow Spring were similar to the other mid-elevation sites.

The species recorded in the seed rain at Lahar I and II were distinct from all other sites (Table 4), as expected given the higher elevation, different surrounding flora, and greater physical exposure of these subalpine sites. Although sampled densities were very low (Table 2), making interpretation speculative, *A. margaritacea* and *E. watsonii* were conspicuously absent from the seed rain although *E. angustifolium* was present. Species characteristic of the surrounding subalpine flora that were recorded at Lahar I and II, but were rarely trapped elsewhere, included *Spraguea umbellata* Torr. (*Calyptridium umbellatum*) (Torrey) E. Greene; *Polygonum newberryi* Small, *Aster ledophyllus* A. Gray, *Lomatium martindalei* (J. Coulter & Rose) J. Coulter & Rose, *Juncus parryi,* and *Hieracium gracile* Hook. (Table 4). *Eriogonum pyrolifolium* Hook., a dominant species in many subalpine sites on Mount St. Helens (del Moral and Wood 1986, Chapin and Bliss 1989, del Moral 1993), was not recorded in the seed rain.

DISCUSSION

Seed rain is a critical factor in determining species composition and abundance in early primary succession on Mount St. Helens. All species in the seed rain with >1% relative abundance at any site are present in the vegetation, and the most common species in the seed rain were also the most common species in the vegetation during the study period (Wood and del Moral 1988; del Moral 1993; del Moral and Wood 1993a; see also Stöcklin and Bäumler 1996). No species with consistent, relatively abundant seed rain appeared to be excluded from establishing at least some individuals on Mount St. Helens due to a lack of ecological tolerance. However, the absolute abundance in the vegetation on Mount St. Helens is determined by a host of other factors in addition to seed rain density including safe-sites for germination (Wood and Morris 1990; del Moral and Wood 1993b; Titus and del Moral 1998) and facilitation (Morris and Wood 1989; del Moral and Wood 1993a). Most of the common species in the seed rain have seeds adapted for wind dispersal: a feathery coma in *Epilobium angustifolium* and *E. watsonii,* and pappuses in *An-*

aphalis margaritacea, Hypochaeris radicata, Hieracium albiflorum, and *Senecio sylvaticus.*

The consistency in species composition of the seed rain among both years and sites suggests that the vegetation will also be similar from site to site, with the exception of the subalpine lahar sites. This prediction is upheld for sites of similar elevation except where patches of *Lupinus lepidus* have developed (del Moral et al. 1995). The species composition of the seed rain also gives some indication as to seed sources. Seeds of common montane species such as *Anaphalis margaritacea, Epilobium angustifolium, E. watsonii* (*E. ciliatum*), *Hypochaeris radicata, Hieracium albiflorum,* and *Senecio sylvaticus* probably originated in seared and blowdown forest 10–20 km to the west and north of the study areas (Fig. 1) where recovery of these species occurred relatively rapidly (Halpern et al. 1990). Westerly prevailing winds likely transported these species up the Toutle River valleys to the Pumice Plains sites (Fig. 1). Willson (1993) reports a wide range in maximum dispersal distances of herbaceous species with wind dispersal adaptations, from a few m to >4000 m. The dispersal ability of *Epilobium* in particular is extraordinary—Solbreck and Andersson (1987) estimated the maximum dispersal distance of *E. angustifolium* to be hundreds of km under windy conditions. Seeds of the ruderal species in the seed rain such as *Cirsium arvense* (L.) Scop., *C. vulgare, Taraxacum officinale, Sonchus asper, Lactuca muralis,* and *Senecio vulgaris* probably had their origin in low-elevation clearcuts or agricultural fields tens of km to the west. Dale (1989) captured several of these same ruderal species at lower elevation on the debris avalanche along the Toutle River to the west.

The only shrub or tree species trapped besides *Salix* was one seed of *Acer circinatum,* in a sample of >75,000 seeds. Since the montane sites on Mount St. Helens will, in the absence of another eruption, eventually succeed to a coniferous forest, the low abundance of late-successional woody species suggests a strong seed dispersal limitation. Similarly, Chapin et al. (1994) detected no spruce seeds and negligible alder seeds in the pioneer stage of primary succession at Glacier Bay at dispersal distances comparable to those of this study (approximately 10 km from seed sources for spruce and 3 km from alder sources). Although not detectable in the seed rain, conifer and shrub seedlings such as *Pseudotsuga menziesii, Abies amabilis, Tsuga heterophylla, Pinus contorta* Loudon, *Alnus sinuata* (Regel) Rydb. (*A. viridis* (chain) DC), *Rubus* spp., and *Vaccinium* spp. do occur in low numbers at most of the sites sampled here (see also del Moral et al. 1995). These individuals are either establishing from extremely low seed source inputs and/or our seed trap design did not adequately sample their mode of dispersal (see below).

Seed traps were designed to estimate the seed rain onto relatively flat, open ground. True densities

may exceed our estimates in microsites where seeds accumulate, such as in depressions or wet sites, or about rocks (Dale 1989; Titus and del Moral 1998). Higher densities also may occur in vegetated sites where short-distance dispersal supplements the long-distance seed rain. For example, at Willow Spring and Lupine Patch, seeds produced on or near the site probably equaled or even exceeded the number of seeds arriving by long-distance dispersal. Also, variation among traps was highest at Willow Spring, with standard errors of 29% and 30% of the density means for 1989 and 1990, respectively (Table 2). This suggests that established vegetation islands augment the long-distance seed rain in a patchy manner, in contrast to barren sites which receive a more predictable, albeit low input.

The sharp decline in the seed rain of *Senecio sylvaticus* (Tables 3 and 4) may be explained by its life history—a biennial, it exploits forest clearcuts for only one or two generations before being outcompeted by more aggressive seral species (West and Chilcote 1968; Halpern et al. 1997). The 1980 eruption of Mount St. Helens apparently created brief but favorable growing conditions for *S. sylvaticus* in surrounding forests that resulted in a pulse of seed rain in 1982 and 1983.

The overall mean density of 33.6 seeds 0.1 m^{-2} yr^{-1} for mid-elevation barren sites on Mount St. Helens is similar to that found by Ryvarden (1971; calculations from Rabinowitz and Rapp 1980), who reported 34.2 to 65.3 seeds 0.1 m^{-2} yr^{-1} for primary succession at the base of a retreating glacier in Norway, and to that of Stöcklin and Bäumler (1996) who found 12.5 seeds 0.1 m^{-2} yr^{-1} for newly exposed terrain in glacial forelands in Switzerland. Archibold (1980) reported 240.0 to 380.0 seeds 0.1 m^{-2} yr^{-1} in stripmine wastes in Saskatchewan, but this higher figure may be due to the closer proximity of seed sources. The very low mean density of 2 seeds 0.1 m^{-2} yr^{-1} for the subalpine lahar sites was probably because seeds of well-dispersed species such as *Anaphalis margaritacea* and *E. watsonii* did not reach that elevation, and because seeds of species in the surrounding vegetation have poor adaptations for dispersal (Wood and del Moral 1987).

Many species that occur in the vegetation on Mount St. Helens were not recorded in the seed rain. Most of these species are uncommon or rare. This suggests that either their seed rain is below our detection limits or that their mode or timing of dispersal is such that they eluded capture. Although we think that low species richness in the seed rain is more likely, our traps were designed to capture wind-dispersed seed and thus may have missed capturing seeds of species with other dispersal modes. One possible dispersal mode that may be important on Mount St. Helens is that of secondary wind dispersal across hard snow surfaces. Matlack (1989) showed that seeds of *Betula lenta* were dispersed greater distances by secondary dispersal

than by primary dispersal to the ground. Because Mount St. Helens receives abundant winter snow and freeze-thaw cycles are common, hard surfaces conducive to secondary dispersal by wind probably occur. Water dispersal (hydrochory) is another unmeasured variable. In addition to permanent streams, numerous small temporary streams commonly develop during spring snowmelt and fall rains, and sheet flow occurs during particularly heavy rains. Seeds can be transported along these watercourses (Stöcklin and Bäumler 1996). Either secondary dispersal or water dispersal may be responsible for the spread of non-wind dispersed species such as *Lupinus lepidus* and the occurrence of the late successional woody species listed above. Animal dispersal (zoochory) is another unmeasured vector. We consider animals to be less important than either wind or water, but we cannot rule out their effect. Plant taxa with fleshy fruits are rare on Mount St. Helens (e.g., *Vaccinium, Rubus*; del Moral 1993) suggesting that frugivory as a means of seed dispersal is also rare. However, birds and large mammals such as elk and coyotes travel long distances to the study sites and may disperse seeds by defecation or transportation in their feathers or hair. The potential importance of a rare colonization event that results in local seed production and population spread should not be underestimated.

Whereas relative abundance of a species in the seed rain is a good indicator of its relative abundance in the vegetation, the reverse is not necessarily true. A few species are common in the vegetation but uncommon in the seed rain. These include *Lupinus lepidus, Salix* spp., and *Eriogonum pyrolifolium*. Lupine is the species with the greatest disparity between its estimated seed rain density and its abundance. Lupine survived the eruption in a variety of high elevation sites around the volcano (del Moral 1983, 1993; del Moral and Wood 1986) and was present on the Pumice Plain as early as 1981 (C. Crisafulli personal communication), possibly establishing from seeds or root fragments washed down from high-elevation survivors. Now lupine occurs across the Pumice Plain and other sites on Mount St. Helens (Morris and Wood 1989; Bishop and Schemske 1998; Titus et al. 1998). In spite of this early record of population growth, seeds of *L. lepidus* were not captured in the seed rain until 1989, presumably because of its limited seed shadow. Lupine seeds have no obvious dispersal adaptations except for ballistic dispersal when legumes dehisce, but this type of dispersal probably only achieves a few m (Willson 1993). Thus the rapid increase of *L. lepidus* on the Pumice Plain was due to vigorous seedling recruitment in close proximity to early colonists, not to long distance dispersal (Wood and del Moral 1988; Morris and Wood 1989). The low abundance of *Salix* spp. in the samples is probably due to a flaw in the sampling design. *Salix* began reproducing as early as 1985 at Willow Spring (Wood personal observa-

tion) but each year due to impassible roads our traps were put out too late to catch dispersing willow seeds. The high abundance of *Salix* around Willow Spring would undoubtedly have contributed greatly to the seed rain at this site and would have resulted in lower relative abundances of other species such as *E. watsonii. Eriogonum pyrolifolium,* a dominant subalpine species, has relatively heavy, round seeds with no obvious dispersal adaptations (Wood and del Moral 1987) and thus its seed shadow apparently did not extend to the seed traps.

The vast majority of incoming seeds in the seed rain fail to establish. Vegetation remained generally sparse by 1990 in spite of a rain of hundreds of seeds m^{-2} yr^{-1} onto most sites. Previous studies demonstrated that limits to abundance on Mount St. Helens are set by environmental factors. Morris and Wood (1989) and del Moral and Wood (1993a) showed that *Lupinus lepidus* may facilitate the establishment of several species including *Anaphalis margaritacea, Epilobium angustifolium,* and *Hypochaeris radicata.* Wood and Morris (1990) showed that manipulation of substrate moisture and microtopographic heterogeneity positively affected the rate of establishment of *A. margaritacea* and *E. angustifolium.* Del Moral and Wood (1993b) showed that most species on the Plains of Abraham established in favorable microsites more often than expected by chance. There is also a tradeoff between seed mass and probability of establishment— heavier seeds have a greater likelihood of establishing on Mount St. Helens due to increased seedling vigor but are less likely to disperse a long distance (Wood and del Moral 1987; Wood and Morris 1990). Titus and del Moral (1998) further demonstrated the importance of microsites in seedling establishment. Thus, the vegetation of early primary succession on Mount St. Helens is composed primarily of well-dispersed species in low abundance. Stochastic events such as chance colonization of species with low long-distance seed rain result in heterogeneous communities with little structure (del Moral et al. 1995). As succession proceeds, community composition will become increasingly uncorrelated with the long-distance seed rain.

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ENVIRONMENTAL GRADIENTS AND VEGETATION STRUCTURE ON SOUTH TEXAS COASTAL CLAY DUNES

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ABSTRACT

Clay dunes are unusual geological features that occur near playas, lagoons, or flats that are sometimes wet but dry out annually. If the sediment in these ephemeral bodies of water contains clay, and if there are strong prevailing winds, flakes or granules of clayey material are transported during the dry season and are caught by edge vegetation. The clay particles moisten in the dew or rain and stick together, eventually creating dunes that support vegetation. Known locally as *lomas,* the clay dunes along the Gulf coast of Texas and Mexico reach their greatest stature near the mouth of the Rio Grande River, where this study was carried out. These dunes support ecologically unique vegetation assemblages. They sit, like islands, in hypersaline lagoons. Sharp environmental gradients separate halophytes from typical coastal thornscrub vegetation. Endangered animal species such as ocelots live in the thornscrub. Development pressures along the border threaten their existence, and the construction of artificial *lomas* has been proposed. In this paper I characterize four *loma* plant communities. The first community is found in the adjacent hypersaline *Flats,* and is limited to halophytes. The second community is found in lower but still elevated salinities at the *Edge* of the *lomas.* At low salinities atop the *lomas* are the dense *Thornscrub* community, and a *Mixed Halophyte and Thornscrub* community that is hypothesized to be the result of disturbance. Analysis of elevation and salinity at plots along transects through the *lomas* allows me to correlate individual plant species with salinity preferences and community membership. An interesting outcome is that while a number of species have fidelity to one community type, there are quite a few bridging species that are found in two community types. This information has important implications for the degree of precision required when attempting to restore or create the clay dune ecosystem.

The clay dunes that occur along the Laguna Madre on the southern part of the Texas Gulf coast are interesting both geologically and biologically. Clay dunes are found in association with playas in west Texas and New Mexico, and are reported in Australia and Africa. The coastal clay dunes described in this paper reach their greatest stature and number near the mouth of the Rio Grande River and decrease to the north and south. Similarly, the vegetation of the south Texas delta of the Rio Grande is unique and in some places luxuriant, but diminishes as the distance from both the river and the Gulf increases.

The clay dunes, or *lomas* as they are known locally, are rendered more exotic by the fact that they exist as low hills with non-halophytic vegetation, sitting in the middle of extensive hypersaline wind tidal flats or lagoons. The lagoons are periodically inundated by wind tides or hurricanes, but are subjected to long periods of drying in the hot south Texas climate. Salts concentrate and the surface of the lagoons may become dry. In addition to the salinity and periodic droughts, there is a persistent brisk wind out of the southeast for much of the year. In this semiarid, semitropical climate, the warm months may be generally described as any but January and February, and even during these months, daytime temperatures above 30°C are common.

Lomas near Boca Chica, the beach north of and adjacent to the mouth of the Rio Grande River, are covered with thornscrub vegetation, some of which is commonly found over much of the Tamaulipan biotic province. In addition, species characteristic of the *lomas* and other coastal areas are found, including *Citharexylum berlandieri* Robins., *Maytenus texana* Lundell, *Prosopis reptans* Benth., *Echeandia chandleri* (Greenm. & Thomps.) M. C. Johnst., *Monanthochloe littoralis* Engelm., and *Yucca treculeana* Carr. Most of the *lomas* in the Boca Chica area are named, and the site for this work is called *Loma Tio Alejos.* It has a roughly north-south orientation, is 200 to 300 meters wide by 600 meters long, and rises about 7.5 m out of a lagoon, which is at an elevation of about 1.5 m. The south end of the *loma* is 300 meters north of a bend in the Rio Grande River; the east side is about 12 km from the Gulf of Mexico. This site and much of the surrounding land is now part of the Lower Rio Grande Valley National Wildlife Refuge.

It has long been known that non-halophytic vegetation grows on *lomas,* and that hypersaline marshes and flats surround them. They are recognized as a unique biotic community by the U.S.F.W.S., and are included in a proposed wildlife corridor running down the Rio Grande and up the coast. One impetus for this study is the extensive restoration program in place on the L.R.G.V. National Wildlife Refuge and the potential for con-

structing or restoring *lomas* to create habitat. Off-refuge, there are significant pressures from en-croaching commercial and residential development and from the proposed construction of a new international bridge and its infrastructure 8-km west of this site.

Knowledge of typical vegetation composition on *lomas* and the relationships among vegetation, *loma* elevation and soil salinity are critical to understanding what controls the vegetation structure. *Loma* vegetation is known to be dense, and often much shorter than it would be in other locations. In this study I measured vegetation composition, woody plant height and density, canopy cover, elevation and soil salinity in quadrats along transects across *Loma Tio Alejos*. Ordination and classification analyses were performed on cover data. The nature of the relationship between *loma* elevation and salinity was determined, and species affinity to sites was related to salinity and elevation.

Clay dunes. The clay dunes along the Gulf Coast in southern Texas have been remarked upon almost since the first accounts of the exploration of the area, probably because these explorations sought river mouths and disembarked from coastal areas. Coffey (1909), while on a soil survey of the region for U.S.D.A., saw the dunes and hypothesized that they were formed by granules of clay, which were blown off the surface of dried lagoons during hot, windy summers. The particles blew to the edge of the lagoon, were caught by vegetation or by wrack or debris, and began to accumulate. Rainfall or the humidity of the nights caused the particles to coalesce. Coffey further noted that they were found near the Rio Grande because the rains are seasonal and lagoons dry out; in more humid climates such conditions do not occur. Foscue (1932) noted that the dunes looked like small islands covered with brush. Huffman and Price (1949) and Price and Kornicker (1961) compared clay dunes all along the Texas and Mexican coast and determined that they existed along the mainland coast from Soto la Marina River in Tamaulipas, Mexico to St. Charles Bay (at the Aransas National Wildlife Refuge) in Texas. The dunes are highest at the Rio Grande (10 m), and become lower (1 m) in the more humid climates to the north and south. These authors essentially agreed with Coffey about the formation of the dunes, adding that they probably grow only during hot months (March to November), retain a loosely porous structure, and represent about 5000 years of growth since beginning of the current still-stand of sea level. During a seven year period of drought in the fifties, about a foot of loosely consolidated pellets accumulated. Their height made the dunes attractive camp sites for the coastal Indian tribes that fished in the area. Aboriginal artifacts occur from about mid-dune to near the top foot, and European artifacts occur near the top. In addition to their use by humans, the endangered ocelot (Tewes 1982) also uses clay dunes.

Tamaulipan Thornscrub. Brown (1994) describes the Tamaulipan biotic province as being one of several provinces that are semidesert scrublands. Such systems are dominated by thorny shrubs and small trees, and characterize much of the world's tropic-subtropic zones. They are found in Australia (*mulga*), southern Africa (bush), South America (*chaco-seco*), Mexico (*matorral*) and Texas (*chaparral*). They are drought-deciduous communities that occupy a position on a moisture gradient somewhere between desert scrub and woodland or forest. They often have an irregularly layered overstory between 2 and 8 m in height, and are typically composed of spinose, microphyllous, and succulent life forms. Thornscrub is often in competition with grassland, and may increase under grazing pressures, with fire suppression, or on poorer soils.

Muller (1947) observed that east central Coahuila, southern Texas, northern Nuevo Leon and northern Tamaulipas all have a vegetation form that is similar. Shreve (1917) called it Texas semi-desert. Muller proposed that it be called Tamaulipan thorn shrub. The more luxuriant and tree-dominated forms found in south Texas and Tamaulipas were called Tamaulipan thorn forest. These environments differ from the adjacent Chihuahuan desert shrub in that they are found at lower elevations, have more rainfall, and are exposed to winds from the Gulf of Mexico. With these habitat differences are also found more thorny shrubs, an abundance of grasses, more luxuriant growth of shrubs, a richer flora, and more numerous characteristic species. With the increase in species there is also a greater number of variants of the vegetation formation.

Blair (1950) included the area in Texas south of the Balcones fault line (which runs from Austin through San Antonio) in his Tamaulipan province. He described the biota of the province as neotropic, strongly diluted by Sonoran biota characteristic of the southwestern U.S. and parts of Mexico, and by biota characteristic of the forests blanketing the Gulf coastal plain. The climate is semiarid and megathermal. From the coast westward, the brush thins as available moisture declines. In Cameron County, at the southern tip of the state, average annual precipitation is just above 25 inches. Mean maximum temperature is 95° in July, mean minimum is 51° in January. Rainfall peaks during tropical storm season (centered on September). Long periods of drought, during which there is little or no rain for 4–6 months, are common; periods during which drought years occur for 3–5 years in succession are also common. A strong, persistent hot wind blows out of the southeast for much of the year.

Probably the earliest exhaustive description of the thornscrub vegetation of the Rio Grande delta was given by Clover (1937). Later Blair (1950), in

his delineation of the biotic provinces of Texas, would call the area on the floodplain the Matamoran district of the Tamaulipan Biotic Province. Clover justified the use of the term *chaparral* for the shorter vegetation of the area, saying that it referred to *chaparro prieto* (*Acacia rigidula* Benth.). *Mesquital* is the term used for *Prosopis glandulosa* Torrey-dominated communities, and *sacatal* for grasslands. Currently, two general types of brush habitats are recognized in the area. The first is referred to as riparian and scrub forests (associated with the Rio Grande, and producing taller vegetation); the second is upland thornscrub and thorn woodland (Jahrsdoerfer and Leslie 1988).

Clover (1937) described the vegetation of the clay dunes near the coast as being similar to salt-affected thornscrub nearby, but being composed of shrubs twisted by the heavy winds. Dominants listed were *Pithecellobium ebano* (Berl.) C. H. Mull., *Leucophyllum frutescens* (Berl.) I. M. Johnst., *Ziziphus obtusifolia* (Torrey & A. Gray) A. Gray, *Castela texana* (T. & G.) Rose, *Randia rhagocarpa* Standl., *Forestiera angustifolia* Torr., *Prosopis glandulosa* Torr. and *Celtis pallida* Torr. Between the clay dune "islands" and the main *chaparral-mesquital* was a transition zone and *sacahuistal* (dominated by *Spartina spartinae* (Trin.) Merr.). USFWS (1997) added *Citharexylem berlandieri, Erythrina herbacea, Dalea scandens* (Mill.) R. T. Clausen, *Echeandia chandleri* and *Sporobolus tharpii* Hithc. as being found exclusively in or near the *loma*-coastal brushland community. Johnson (1963) added that the windward sides of some of the dunes were covered with a thick growth of *Sporobolus wrightii* Scribn. (*sacatón*).

METHODS

In late October 1998, I began the establishment of two transects across *Loma Tio Alejos*. The first transect ran approximately east-west. It started in an unvegetated area of hypersaline lagoon to the west of the *loma*, crossed 200-m of halophytic vegetation, encountered the southern part of the *loma* and entered thornscrub vegetation. It climbed for the next 100 m to the ridgeline and then dropped, over the following 100-m, to the edge of halophytic vegetation on the east of the *loma*. The transect then ended after it traversed 30 m of the halophytic vegetation. Rather than being symmetrical, the *loma* is kidney-bean shaped, so that transect two could be oriented in a north-south direction and cross the north end of the *loma* almost perpendicular to its axis.

The second transect was finished by the beginning of December. It started on the south side of the north end of the *loma* and traveled for 30 m in halophytic vegetation, then entered the brush and traveled 80 m to the ridgeline. It then went down through a depression and up to another ridgeline, traversing extremely dense brush for about 70 m.

The transect descended through thornscrub for 70 meters and was terminated about 50 m into the halophytic vegetation to the north of the *loma*.

Distance along transects was measured with surveying tapes, and station stakes were placed every ten meters (stations 0+00, 0+10, etc.). Differential leveling, employing a Keuffel and Esser optical level, was used to determine relative elevations along each transect. Elevations on transect one were tied to elevations on transect two by closing a leveling loop from one transect to the other along a trail which ran down the ridge of the *loma*. The elevation of the transects was then fitted to a USGS contour map of the *loma* and elevations from that map were used to register the high and low points surveyed.

Vegetation was sampled in 10 × 20 m quadrats along most of both transects vegetation was so thick from station 0+20 to station 2+00 along transect 2 that it was sampled using 5 × 20 m quadrats oriented with their long axis parallel to the machete-cut line through the brush. By the conclusion of the investigation, 57 quadrats were measured and 76 plant species were found. In each quadrat the percent cover of herbaceous species was recorded, as well as the number of species, the number of individuals of each woody species, height and two crown-width dimensions for woody species. Cover for woody species was calculated by averaging the two dimensions and calculating the area of a circle with this average as the diameter.

Soil samples for salinity measurements (Abbott 1967) were taken from each quadrat using a 3.8-cm diameter corer. Cores were generally 10–15 cm long, and were taken after removing organic matter and debris from the soil surface. Cores were extruded onto a tray and the length of each sample was measured, allowing the calculation of soil volume. Wet weight of each core was measured, all were oven-dried at 80°C, and dry weights were measured. Dried cores were placed in flasks and a volume of water twice the original volume of the cores was added to each. The flasks were sealed with rubber stoppers and agitated for three days. They were then allowed to settle in a cold room for three days and the clear supernatant was removed with a syringe.

Osmolality of the soil extract was measured with an Advanced Instruments Model 3300 Micro Osmometer (Advanced Instruments, Inc, Two Technology Way, Norwood, MA 02062). From the osmolality of the soil extract, values were calculated for the osmotically active solutes per unit volume of soil ("a" below) and the apparent salinity of the soil solution at the time the sample was taken ("e" below) (Mahall and Park 1976). The following calculations were made to arrive at these two values.

$$a = \frac{b \times c}{d} \qquad e = \frac{b \times c}{f}$$

where   a = osmotically active solutes per unit
              volume of soil (m-osm. ml^{-1});
         b = osmolality (m-osm. ml^{-1} water) of
              soil extract (from freezing point
              depression);
         c = volume of water added to dry soil
              core (ml);
         d = original volume of soil core (ml);
         e = apparent salinity of soil solution
              (m-osm. g^{-1} water);
         f = weight of water in soil core (g).
The soil solution salinity was converted to ppt for
figures.

Two data sets, one containing species cover information for each quadrat and the second containing elevation and soil salinity data at each quadrat were entered as the primary and secondary matrices in the multivariate software package PC-Ord (McCune and Mefford 1997). Classification was performed using TWINSPAN, and ordination was performed using DCA (detrended correspondence analysis), which uses the stand species matrix; the joint plot option was used to overlay environmental variable vectors over the DCA-generated ordination plot.

TWINSPAN is a divisive classification technique that divides all initial stands in an analysis into two groups using an ordination, then iteratively refines the division. Each group formed is then divided into two new groups. (Jongman et al 1987). The mechanical division of existing groups can go on until some stopping rule is triggered (maximum number of divisions or minimum number of stands in a group may be specified). The actual selection of what divisions to accept may depend upon whether further divisions add to the explanatory power of the analysis (Gauch 1982). In this analysis, four groups were used because each of the four groups represented a homogeneity of species composition and was characterized by similar dominant species.

RESULTS

Elevation. The elevation of the saline flats around the *lomas* in this area is about 1.5 m, USGS datum. On this *loma,* over a distance of 100–150 m, the measured transects rose to about 6.5–7 m at the height of land, then dropped again (Fig. 1). The elevation of the highest point on the *loma* was estimated at about 9 m.

Vegetation. Seventy-six species were found within the sampling quadrats along the two transects across *Loma Tio Alejos.* Twenty-seven of them were erect, woody plants. There were also 8 grasses, and a number of halophytes, weedy herbaceous species, and herbaceous understory species. *Echeandia chandleri,* a lily limited to clay soils in south Texas and described as rare (USFWS 1997), was common here. *Ophioglossum vulgatum* L., a vascular cryptogam, was found growing under *Pro-*

sopis glandulosa trees. The vegetation gradient from the saline flats to the thornscrub of the *lomas* was short and steep, but there was surprising overlap of thornscrub and halophytic species.

Vegetation composition and cover data were analyzed using multivariate analysis. Classification of stands and species was accomplished using TWINSPAN. One of the products of a TWINSPAN analysis is a joint ordination of stands and species called a two-way table. The species list from a two-way table is ordered, i.e., the species that are on either end of the list are usually found in completely different environments and species which are next to one another on the list are usually found together. On the list in Table 1, species at the top are from sites near the highest elevations of the *loma,* while species at the bottom occur mostly in the adjacent flats and at the *loma* edges.

I elected to stop the TWINSPAN procedure after four groups of stands had been generated because each of the four groups represented a relatively homogeneous association of species and was characterized by a unique dominant species or group of dominants. I will describe the important species, the location of stands, and the general environment in which each group occurs.

The first division segregated the high-diversity, non-halophytic thornscrub vegetation into one group. Woody thornscrub species and their associated herbaceous understory or gap species dominate it. The other group from this division includes all of the species known to be halophytic, but halophytes are not limited to the second group.

The second division divided stands in the thornscrub vegetation group into two smaller groups, one of which is made up of species characteristic of more widely distributed coastal upland sites. All of the sites in this subgroup are found on the higher elevations of the north transect; the vegetation there is characterized by a dense canopy and shortened stature. On Figure 2, this association is called "*Thornscrub*". The other subgroup in this division includes more salt-tolerant thornscrub which is found on the lower ends of the north transect and on the south transect. On Figure 2 this association is called "*Mixed Thornscrub and Halophytes*". Indicator species for the group are *Prosopis reptans, Maytenus texana* Lundell. and *Ericamera austrotexana* M. C. Johnst. Almost all of the *Yucca treculeana* Carr. and *Prosopis glandulosa* are also found in this grouping. This second subgroup could be further divided into closed canopy and open canopy groupings, which would have slight species differences.

The third division divides the stands containing mostly halophytic vegetation into two subgroups. The first subgroup is the association that makes up the low shrubby vegetation around the edges of the *loma.* On Figure 2 this is called "*Edge*". Indicator species for this subgroup are *Borrichia frutescens* (L.) DC and *Lycium carolinianum* Walt. The sec-

NORTH TRANSECT
SALINITY

SOUTH TRANSECT
SALINITY
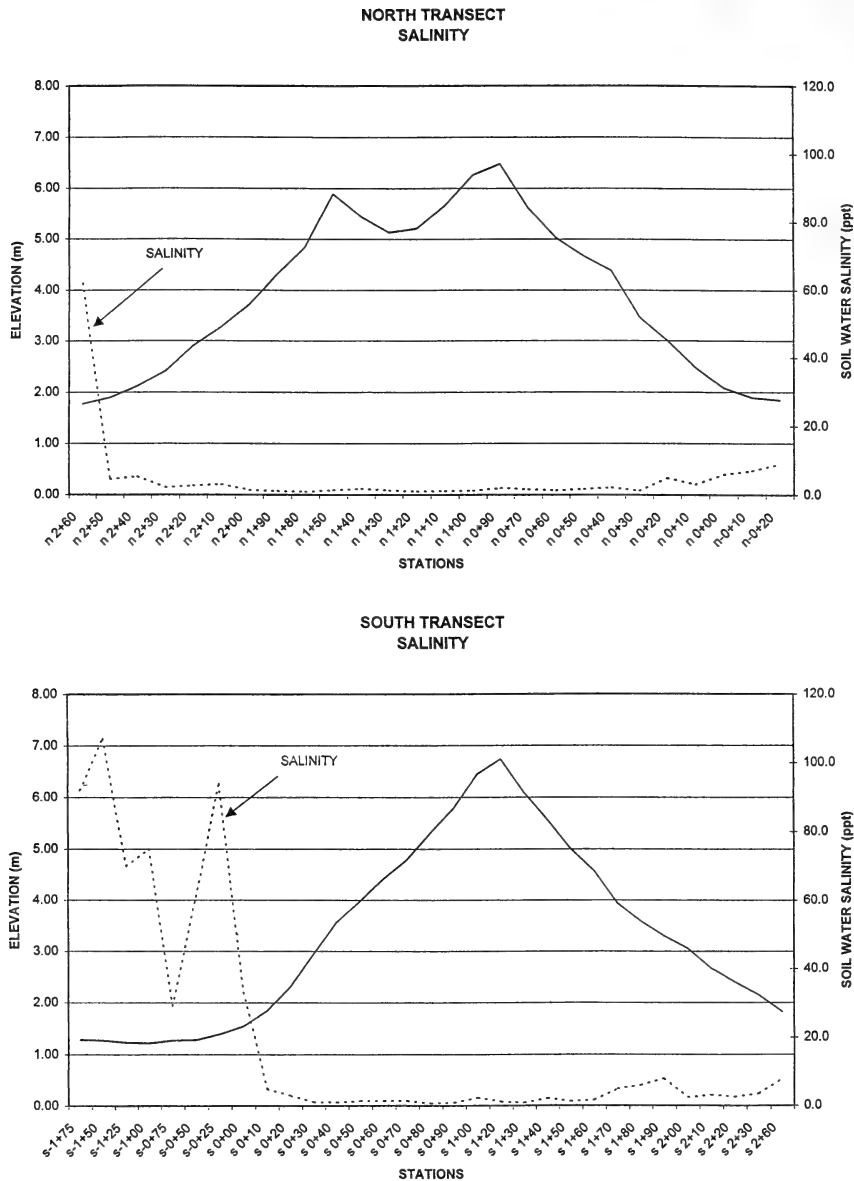
Fig. 1. Elevation and salinity along the north transect (which runs north-south) and the south transect (which runs east-west) across *Loma Tio Alejos*, near the mouth of the Rio Grande River in south Texas. Salinity is represented by a dashed line, elevation by a solid line. The salinity is the apparent soil water salinity obtained by measuring the osmolality of a known volume of water into which a dried soil sample was mixed; salinity at the water content of the soil when the sample was taken was then calculated.

ond subgroup is dominated by three species (*Salicornia virginica* L., *Monanthochloe littoralis* Engelm. and *Batis maritima* L.) and little else; sites making up this subgroup occur in the extremely salty flats surrounding the *lomas*. On Figure 2 this association is referred to as "*Flats*".

The same data set that was used to obtain a classification of stands and species with TWINSPAN was subjected to an ordination analysis. Ordination allows the investigator to plot stands or species in a multi-dimensional space that can be interpreted in terms of environmental variation; Detrended Correspondence Analysis (DCA), an indirect ordination technique, was used. Since an environmental matrix of stands by environmental data (salinity, elevation) was available, the joint plot option of PC-Ord was used to plot environmental vectors on the DCA ordination plots. The first DCA axis had and an eigenvalue of 0.859, indicating that a substantial amount of the variation in the data set was accounted for by this axis. When plotted as a joint plot, the arrow representing salinity was almost

identical to axis one, and the arrow representing elevation, while negatively correlated with salinity, was very close to axis one.

Canonical Correspondence Analysis (CCA) allows the investigator to constrain the ordination axes to some combination of directly measured environmental variables (Jongman et al. 1987). When this was done using elevation and salinity as the environmental variables, the eigenvalue for the first axis was 0.662, which is still high (Jongman et al. 1987). In the CCA analysis the arrows for elevation and salinity were highly correlated with axis 1. The results of these ordinations indicate that elevation and salinity are environmental factors that account for most of the variation in vegetation structure on the *lomas*. They are inversely correlated; as elevation increases, salinity decreases.

Salinity. Salinity was high in the flats but dropped very quickly as the *loma* elevation rose above that of the surrounding flats. (Fig. 1). Salinity per volume of soil and apparent salinity of soil water were highly correlated (r = 0.995), so apparent salinity in ppt will be used to discuss the relationship among elevation, vegetation and salinity. Average soil water salinity in plots in the "*Flats*" vegetation association was 64.1 ± 11.8 ppt. This salinity is significantly (P = 0.05) greater than that in any of the other associations. Mean soil water salinity in the "*Edge*" association, 6.3 ± 1.9 ppt, is higher than that in the "*Mixed*" or "*Thornscrub*" groups, though not significantly so. Mean salinity in the "*Mixed*" group is 2.1 ± 0.4, and in the "*Thornscrub*" group is 2.0 ± 0.3 ppt.

DISCUSSION

The ecotone between the hypersaline flats of Laguna Madre and the coastal thornscrub in south Texas has created interesting and unexpected vegetation associations. The *lomas* or clay dunes are a microcosm of this contact, and they reach their maximum expression near the mouth of the Rio Grande River. Coastal thornscrub on the *lomas* and on the nearby mainland is valued because of its importance as wildlife habitat (ocelots, birds, and butterflies). It is part of a breathtaking diversity of vegetation; Jahrsdoerfer and Leslie (1988) indicated that there were 265 native woody species in the thornscrub of southern Texas. It is the site of scarce and unusual plant species including the species of concern *Echeandia chandleri*, *Citharexylum berlandieri* Robins. and the endemic *Sporobolus tharpii* Hitchc. (Jahrsdoerfer and Leslie 1988). The Laguna Madre is unique in that it is a huge lagoon, which has little freshwater input except from tropical storms. The hot climate, persistent winds and a tendency to experience prolonged periods of drought have created a water body that becomes hypersaline. Many of the *lomas* near the site of this study rise out of wind flats at the edge of the La-

guna Madre; these flats are sometimes inundated but are very salty during most years.

Many of the *lomas* near the mouth of the Rio Grande and behind Boca Chica beach are now protected and part of the Lower Rio Grande Valley National Wildlife Refuge. This refuge and the Laguna Atascosa National Wildlife Refuge on the coast 20 km to the north are both sites of active vegetation restoration programs. Because of the sharp environmental gradients in areas adjacent to salt flats and lagoons, and because of unique tolerances and preferences of plant species which would normally be selected for restoration plantings (in general, dominant and secondary woody species), information about the sorting of species along environmental gradients is important. Since the *lomas* rise like small islands out of low and level salt flats, their elevation was predicted to be an important environmental axis; this proved to be the case. Since *lomas* support species common to sites that are not salt-affected, and because they are surrounded by halophytic vegetation that is tolerant to high concentrations of salts, a salinity gradient was predicted. This also proved to be true.

Other environmental factors may also shape vegetation structure. Winds off the nearby gulf are persistent and may result in dwarfing of vegetation. Soils sampled were generally silty clays or clayey silts, with more clay in soils in the flats. *Lomas* have a history of use by people, and there are roads leading to them, around them and across them. There are excavation sites, dumps, and disturbed areas with weedy vegetation (primary weeds are the introduced pasture and lawn grasses *Cenchrus ciliaris* L., *Cynodon dactylon* (L.) Pers., *Dichanthium annulatum* Stapf. and *Panicum maximum* Jacq.); some of the vegetation plots occurred in these areas. Multivariate analysis indicated that elevation and salinity change explains a very high amount of the variation in vegetation on *Loma Tio Alejos*.

The analysis of data from 57 quadrats along two transects across the *loma* was carried out by performing a classification procedure (TWINSPAN) and an ordination procedure (DCA). As a result of the TWINSPAN analysis, four vegetation groupings or associations were identified. The groups were called "*Thornscrub*", "*Mixed Thornscrub and Halophytes*", "*Edge*" and "*Flats*". The 16 plots in the *Thornscrub* group contained 36 plant species. For *Mixed Thornscrub and Halophytes* the numbers were 20 plots and 67 species, for *Edge* 13 plots and 41 species, and for *Flats* 8 plots and 11 species.

All except one of the plots assigned to the *Thornscrub* group were on the north transect; that one occurred in very thick brush on the south transect. This association is made up of plants in very dense, short (3–4 m) vegetation. Vegetation on the north transect may have been subjected to greater wind intensity, because the south part of the *loma* is partially protected from the wind by vegetation along

TABLE 1. LIST OF SPECIES FOUND ALONG TRANSECTS AT *LOMA TIO ALEJOS*. Species have been ranked by TWINSPAN classification program so that those generally found at the higher elevation, lower salinity sites occur at the top of the list; those found at the lower elevations and in the saline flats are at the bottom. Frequency of occurrence in plots of each of the four TWINSPAN community types at the site (*Thornscrub, Mixed Thornscrub and Halophytes, Edge and Flats*) is shown for each species as a percentage. Numbers of plots of each of the community types are respectively n = 16, 20, 13 and 8.

	Thornscrub	Mixed	Edge	Flats
Castela texana	44	10	0	0
Pithecellobium pallens	6	0	0	0
Malpighia glabra	25	5	0	0
Bastardia viscosa	31	5	0	0
Rivina humilis	50	20	0	0
Celtis pallida	63	30	8	0
Pithecellobium ebano	19	0	0	0
Phaulothamnus spinescens	81	45	8	0
Randia rhagocarpa	69	10	0	0
Lycium berlandieri	13	5	0	0
Aloysia gratissima	13	0	0	0
Citharexylum berlandieri	94	85	8	0
Zanthoxylum fagara	100	85	0	0
Karwinskia humboldtiana	63	35	8	0
Lantana horrida	38	60	0	0
Capsicum annum	6	20	0	0
Schaefferia cuneifolia	25	40	0	0
Passiflora foetida	6	5	0	0
Cissus incisa	44	60	8	0
Forestiera angustifolia	19	30	8	0
Verbesina microptera	38	30	0	0
Zisiphus obtusifolia	13	20	8	0
Isocoma drummondii	19	80	15	0
Allowissadula lozani	19	55	8	0
Yucca treculeana	13	60	15	0
Prosopis glandulosa	25	85	8	0
Eupatorium azureum	50	70	8	0
Leucophyllum frutescens	38	65	8	0
Condalia hookeri	6	10	0	0
Echeandia chandleri	13	25	0	0
Gymnosperma glutinosum	6	10	0	0
Ericameria austrotexana	0	80	8	0
Eupatorium incarnatum	0	20	0	0
Cenchrus incertus	0	10	0	0
Atriplex acanthocarpa	0	5	0	0
Wedelia hispida	0	15	0	0
Physalis cinerascens	0	20	0	0
Ophioglossum vulgatum	0	20	0	0
Acacia farnesiana	0	5	0	0
Trixis inula	0	5	0	0
Dichanthium annulatum	0	40	0	0
Croton cortesianus	0	5	0	0
Sida ciliaris	0	10	0	0
Malvastrum americanum	0	15	0	0
Ibervillea lindheimeri	0	10	0	0
Chenopodium ambrosoides	0	5	0	0
Cenchrus ciliaris	0	50	15	0
Sarcostema cynanchoides	0	30	15	0
Cynodon dactylon	0	10	8	0
Croton leucophyllus	0	10	8	0
Opuntia leptocaulis	6	30	31	0
Trandescantia micrantha	6	10	23	0
Acleisanthes obtusa	6	5	8	0
Borrichia frutescens	13	55	85	0
Oxalis drummondii	0	5	8	0
Solanum eleagnifolium	0	10	8	0
Sporobolus wrightii	0	10	15	0
Panicum maximum	0	5	0	13
Oxalis dichondrifolia	6	15	15	0

TABLE 1. CONTINUED.

	Thornscrub	Mixed	Edge	Flats
Evolvulus alsinoides	0	5	8	0
Maytenus texana	0	75	77	13
Prosopis reptans	0	70	85	25
Machaeranthera phyllocephala	0	45	46	0
Spartina spartinae	0	10	15	0
Suaeda linearis	0	0	23	25
Cressa nudicaulis	0	10	23	25
Salicornia virginica	0	0	23	100
Talinum paniculatum	0	5	8	25
Atriplex matamorensis	0	0	0	13
Lycium carolinianum	0	20	85	0
Limonium nashii	0	0	31	0
Echinocactus setispinus var. setaceus	0	0	8	0
Distichlis spicata	0	0	8	0
Monanthochloe littoralis	0	30	100	75
Opuntia engelmannii	0	10	38	13
Batis maritima	0	5	69	100

the river and by a road berm. Plots assigned to the *Mixed* group occurred in a more disturbed area on the north end of the north transect, and at the upper elevations of the south transect. There was erosion and open areas in both locations, so human disturbance may have been partially involved in the creation of such sites. Since salinity and elevation differences were inconsequential between plots in these two associations, the hypothesis that the *Mixed* association is generated by disturbance should be investigated more thoroughly. Any restoration attempt would create a disturbed environment, and so the *Mixed* association might be the expected mid-successional vegetation type on less-salty soils. *Prosopis glandulosa,* well-known as a self-seeder on open sites in South Texas (Archer et al. 1988), is a dominant species in the *Mixed* association but found in few plots in the more dense *Thornscrub* association.

Plots in the *Edge* association occur in a band about 30–40 m wide around the *loma,* and are visually different from the adjacent brush because they are open, and woody vegetation in them is either short or widely spaced. At the lower and saltier sites in this association, plant diversity diminishes to an average of 4 species per plot, and plants are generally less than a few decimeters tall. The saline *Flats* are characterized by a few species, and in places the salinity may become so great that no vascular plants occur. There was a substantial increase in soil salinity at the interface between the *Edge* association and the *Flats* (Fig. 1). At one unvegetated quadrat in the flats, a soil water salinity of 187 ppt, roughly five times that of sea water, was measured.

The mean soil water salinity of soil samples taken from plots in the *Flats* was 64 ppt, or almost twice the salinity of seawater. The *Flats* are truly the province of halophytes. Localized or general evaporation and concentration probably result in

much higher localized salinity during drought periods. Salinity in the *Mixed* and *Thornscrub* associations, on the other hand, fell under or around the 1.5–2 ppt salinity threshold that is generally considered the point below which crop plants have no salinity problems (Hartman et al. 1990). Salinity in plots in the *Edge* association were generally in the range within which plants are likely to be affected, but not so high as to limit plant composition to halophytes.

Each of the four vegetation associations identified by classification analysis was characterized by a set of dominant species (based upon total cover). In analyzing the species composition of each association, it became evident that there were some species which preferred conditions found in sites limited to one vegetation association, but there were also many species that did quite well in two of the associations. For instance, *Castela texana* (T. & G.) Rose. and *Randia rhagocarpa* (Fig. 2a) were common in *Thornscrub* association and rare in the *Mixed* association. *Citharexylum berlandieri* (Fig. 2b) and *Zanthoxylum fagara* (L.) Sarg. were in both *Thornscrub* and *Mixed* associations. *Yucca treculeana* Carr. (Fig. 2c) preferred the *Mixed* association, while *Borrichia frutescens* (L.) DC (Fig. 2d), *Maytenus texana* Lundell. and *Prosopis reptans* were found in both *Mixed* and *Edge* associations. This combination of species with fidelity to an association and species which overlap associations continued with *Lycium carolinianum* Walt. (Fig. 2e) found in *Edge, Monanthochloe littoralis* and *Batis maritima* L. (Fig. 2f) found in *Edge* and *Flats,* and *Salicornia virginiana* L. (Fig. 2g) found in *Flats.*

All of the species listed by Shindle and Tewes (1998) as recommended for the restoration of ocelot habitat, as well as a broad variety of others, are found on the *lomas.* This paper has presented information about the environmental preferences of *loma* species. The mixing of species which have
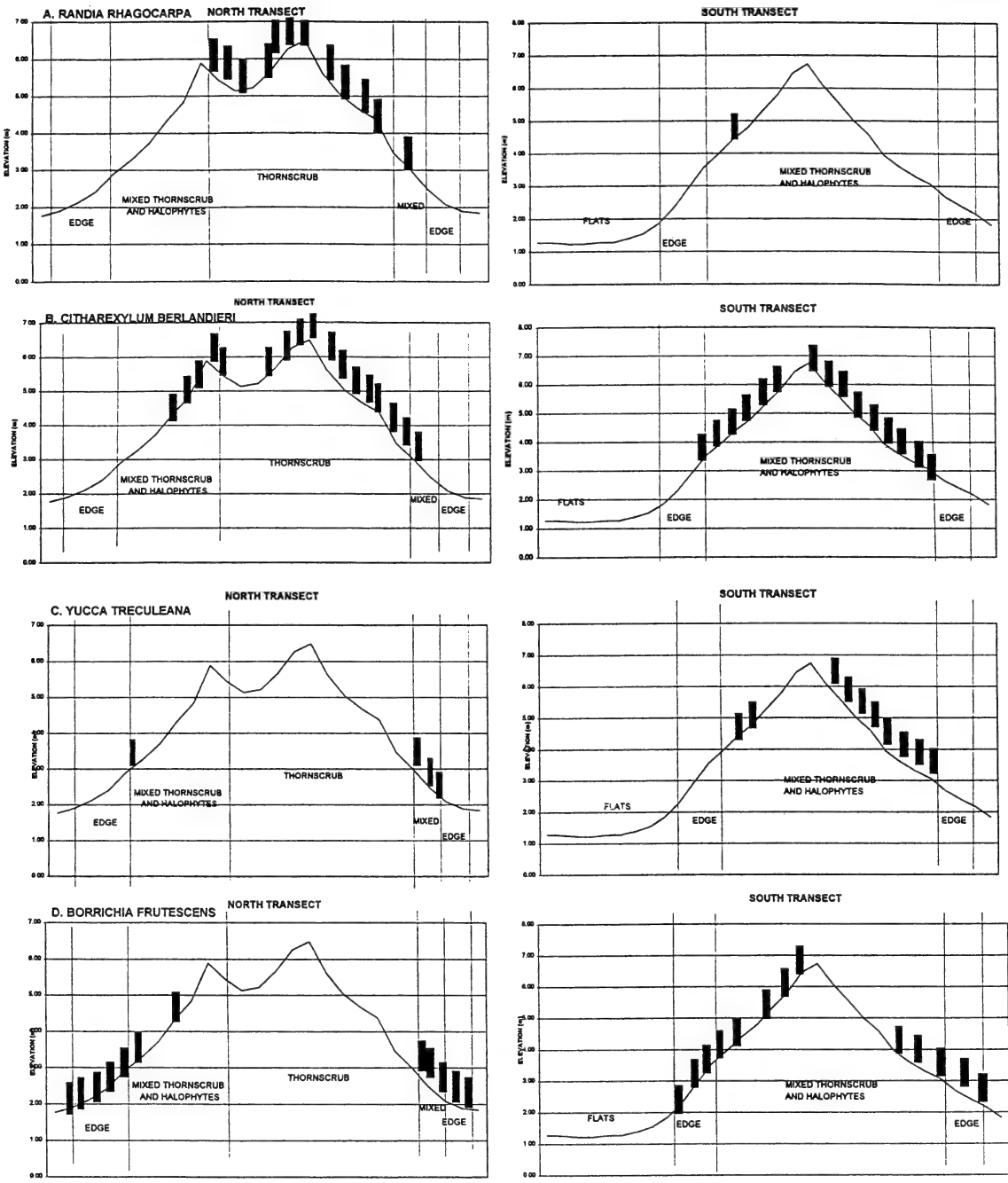
Fig. 2.　Presence of species in plots along transects. A solid vertical bar indicates that the species shown was present in a plot: a.) *Randia rhagocarpa,* occurring primarily in the *Thornscrub* association, b.) *Citharexylum berlandieri,* occurring in both the *Thornscrub* and *Mixed* associations, c.) *Yucca treculeana,* occurring primarily in the *Mixed* association, d.) *Borrichia frutescens,* occurring in both the *Mixed* and *Edge* associations, e.) *Lycium carolinianum,* occurring primarily in the *Edge* association, f.) *Batis maritima,* occurring in both the *Edge* and *Flats* associations, g.) *Salicornia virginica,* occurring primarily in the *Flats* association.

narrow habitat ranges with species which have broader habitat ranges when planting a restoration project is wasteful of plant materials. For the plant installation phase of a restoration project, some spe- cies may be placed on the landscape with less pre- cision, but others require an exact understanding of the species preferences and the site conditions. Plant materials for restoration or creation of *lomas*
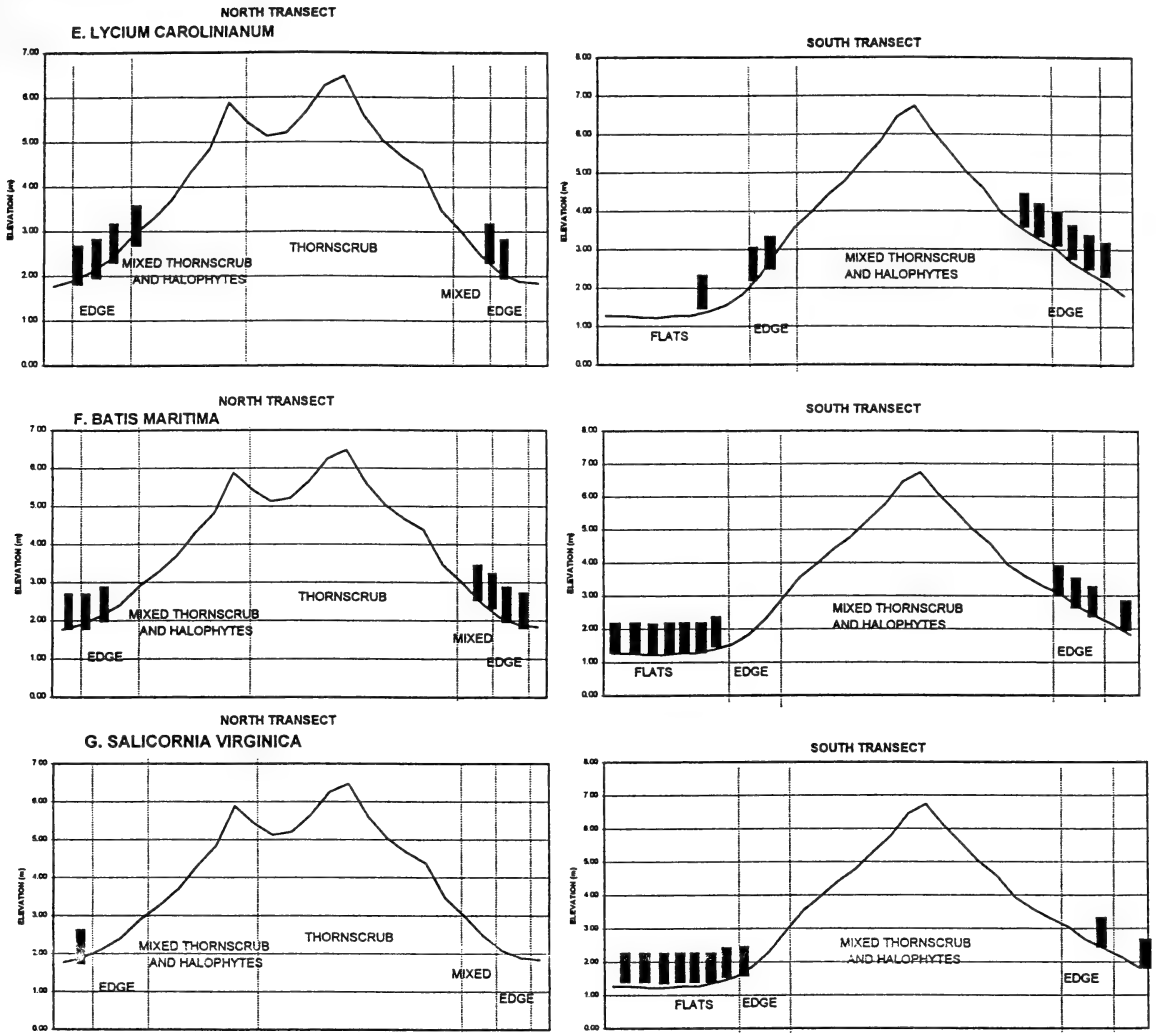
FIG. 2. Continued.

will probably never be abundant, so placement of seedlings or seeds into the proper environmental zone will be critical to the success of a restoration project.

In conclusion, this work has confirmed that coastal clay dunes or *lomas* are unique systems that are persistent over time. Unusual plant associations (thornscrub vegetation and halophytes in close proximity or mixed) and rare and threatened plants (*Echeandia chandleri, Citharexylum berlandieri*) are found on them; their individual vegetation structure can be complex. They are known to be valuable as wildlife habitat. Vegetation structure across *lomas* varies along environmental gradients, which can be predicted for the most part by measuring elevation and salinity. Reports in the literature suggest that wind direction can also be an important factor in vegetation composition and size (Clover 1937). For many centuries, these unique systems have been isolated and not greatly dam-

aged. Population pressure and commercial development now pose a threat to the vegetation systems and the wildlife that they support. Restoration in other areas of south Texas Tamaulipan thornscrub has been undertaken successfully, and the core of an extensive wildlife corridor is being created along the coast and up the Rio Grande River. The restoration or creation of *loma* vegetation to augment habitat and add to the wildlife corridor is an important and achievable element of this restoration.

The ability to restore unique ecosystems like the clay dunes, if indeed we have that ability, does not mean that there is no need for conservation of such unusual habitats. Conservation is an integral part of the U.S.F.W.S. plan for development of a wildlife corridor in south Texas. Important parcels have been identified and a considerable acreage of land upon which dunes sit has been purchased. Restoration can augment the effectiveness of conservation in a number of ways, including the creation of

buffers, the increase in the effective size of a conserved parcel, the creation of corridors, and the initiation of a successional trajectory that will eventually result in an ecosystem that is not much different from one at a conserved site.

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CHROMOSOME COUNTS AND TAXONOMIC NOTES ON *DRABA* (BRASSICACEAE) OF THE INTERMOUNTAIN WEST. 1: UTAH AND VICINITY

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ABSTRACT

Of the 350+ species ascribed to *Draba,* nearly one quarter occur in the Intermountain Region of the western United States. Most of these *Draba* species have not been examined cytologically. This paper presents a total of 18 chromosome counts for 11 different taxa occurring in Utah, Wyoming, and Arizona. The chromosome numbers of *D. juniperina, D. kassii, D. maguirei* var. *maguirei, D. rectifructa, D. sobolifera, D. spectabilis* var. *spectabilis,* and *D. subalpina* are reported here for the first time. Counts differing from published reports are documented for *D. asprella* var. *stelligera* and *D. cuneifolia* var. *cuneifolia.* The taxonomic significance of the new chromosome counts is discussed for each species. Counts of $n = 11$ and $n = 13$ appear to be the first reports of those numbers in the genus, and they complete the continuous series of aneuploid base numbers extending from 8 to 16. It is suggested that the Intermountain West may be a center of diversity for aneuploid *Draba,* and that this assemblage of species provides a unique opportunity to study chromosomal evolution and speciation.

Species assigned to *Draba,* considered to be the largest genus in the Brassicaceae (Rollins 1993), occupy a variety of habitats and occur on all continents except Australia and Antarctica. The group achieves its greatest diversity in topographically complex, mountainous regions where the disjunct occurrence of suitable habitats seems to favor isolation and speciation (Payson 1917). A prime example of this is seen in the Intermountain Region of the western United States, broadly defined here as the territory extending from the continental divide to the Pacific Crest (Sierran-Cascade axis). Of the 350+ species attributed to *Draba* by Rollins (1993), nearly one quarter occur in this region and more than 50% of those are endemic to it.

The Intermountain West is *terra incognita* as far as the cytology of *Draba* is concerned. Of the 57 taxa confined to this region, only 11 have been examined chromosomally. Half of these are known from single counts, and none can be considered adequately sampled. By comparison, 37 of the 40 *Draba* species found in Canada and Alaska have been studied cytologically, thanks in large part to the diligent efforts of G. A. Mulligan (1966, 1970a, b, 1971a, b, 1972, 1974, 1975, 1976).

Mulligan's work on the high-latitude North American species of *Draba* (summarized in the 1976 paper) led to major advances in our taxonomic understanding of the genus. In addition to clarifying species boundaries in several groups, his data provided the basis for the only modern infrageneric classification of North American *Draba.* Setting aside *Draba* (*Erophila*) *verna* L., a Eurasian introduction unrelated to the native species, Mulligan (1976) recognized three informal groups based on a combination of chromosome number, flower color, breeding system, and hybridization studies.

All 17 of the white-flowered species studied by Mulligan exhibit euploid chromosome numbers based on $x = 8$. They clearly are related to Eurasian boreal species assigned by Schulz (1927) to the section *Leucodraba* DC. Another nine Canadian species were assigned to his yellow-flowered euploid alliance, which also frequents boreal habitats and has representatives in Eurasia. The remaining 13 Canadian taxa were placed in a yellow-flowered group characterized by aneuploid chromosome numbers of $n = 9, 10, 12, 14, 15,$ and 37 (Mulligan 1976). Apparently restricted to North and South America, this assemblage of species appears more tolerant of the warm/dry conditions that prevail in much of the western United States.

Mulligan's (1976) informal classification of North American *Draba* is a vast improvement over the patently unnatural sections proposed by Schulz (1927). However, it can neither be used nor evaluated phylogenetically until the chromosome numbers of local *Draba* species have been determined. The goals of this study were: 1) to collect crucial chromosome data for Intermountain *Draba* species, 2) to critically assess current taxonomic treatments for the species sampled, and 3) to develop a set of chromosomally vouchered samples for a DNA analysis (Beilstein and Windham in prep.) designed to test the monophyly of Mulligan's (1976) informal species groups.

MATERIALS AND METHODS

Chromosome counts were made from flower buds of wild plants fixed in Farmer's solution (3

parts 95% ethanol: 1 part glacial acetic acid). Fixed materials were stored at −20°C for up to five years and transferred to 70% ethanol immediately before making slides. Buds (or dissected anthers in larger-flowered species) were macerated in a drop of 1% acetocarmine stain, which was mixed 1:1 with Hoyer's solution prior to setting the cover slip and squashing. Slides were examined with an Olympus BH-2 phase contrast microscope, and representative cells were photographed using Kodak Technical Pan 2415 film. A full set of voucher specimens was deposited at the Garrett Herbarium, Utah Museum of Natural History (UT). Duplicate vouchers were deposited at the herbaria listed in Table 1. To guide the discussion, I produced a compendium of published chromosome counts for all taxa studied and their putative relatives. This list was assembled by running all accepted names and synonyms from Rollins (1993) and Kartesz (1994) through *Chromosome Numbers of Flowering Plants* (Federov 1974) and a complete set of the *Index to Plant Chromosome Numbers* spanning the period 1966–1995 (Omduff 1967, 1968; Moore 1973, 1974, 1977; Goldblatt 1981, 1984, 1985, 1988; Goldblatt and Johnson 1990, 1991, 1994, 1996 & 1998). The primary literature was consulted to verify critical taxonomic and geographic information for each North American count identified by this search.

RESULTS

My chromosome studies of Utah, Wyoming, and Arizona *Draba* species yielded a total of 18 counts for 11 different taxa (Table 1). Seven of these taxa have not been counted previously. These include *D. juniperina* Dorn ($n = 11$), *D. kassii* Welsh ($n = 11$), *D. maguirei* C. L. Hitchc. var. *maguirei* ($n = 16$), *D. rectifructa* C. L. Hitchc. ($n = 12$), *D. sobolifera* Rydb. ($n = 13$), *D. spectabilis* Greene var. *spectabilis* ($n = 10$), and *D. subalpina* Goodman & C. L. Hitchc. ($n = 13$). Counts for two of the remaining taxa, *D. asprella* Greene var. *stelligera* O. E. Schulz ($n = 15$), and *D. cuneifolia* Nutt. ex. T. & G. var. *cuneifolia* ($n = 15$), differ from numbers previously reported in the literature. Unexpected counts, especially those that disagree with the literature, are documented photographically in Figures 1–6. Determinations of $n = 11$ and $n = 13$ appear to be the first reports of those numbers in the genus, and they complete the continuous series of aneuploid base numbers extending from 8 to 16. In fact, this small sample of taxa includes every step in that aneuploid series except $n = 9$ and $n = 14$.

DISCUSSION

The plants herein referred to *Draba albertina* Greene originally were identified as *D. stenoloba* Ledeb. based on the treatment in *A Utah Flora* (Welsh 1993). Because *D stenoloba* has a chromosome number of $n = 20$ (Mulligan 1975), I was surprised when samples from two widely separated Utah populations yielded counts of $n = 12$ (Fig. 1) and $2n = 24$. These determinations agree with previous reports for *D. albertina,* including four counts from Alberta and one from the Northwest Territories (Mulligan 1975). An additional count of $n = 12$ from Wyoming originally attributed to *D. stenoloba* (Mulligan 1966) was reassigned to *D. albertina* in a subsequent paper by Mulligan (1975).

Prior to detailed studies of the group (Mulligan 1975), *Draba albertina* was treated as a synonym or variety (*nana*) of *D. stenoloba.* After discovering that the two taxa had different chromosome numbers, Mulligan recognized them as separate species based on correlated morphological and geographical differences. The decision to classify these taxa as species also is supported by artificial hybridization experiments (Mulligan 1975), which indicate that any hybrids formed are completely sterile.

According to Mulligan (1975) and Rollins (1993), *D. stenoloba,* with a chromosome number of $n = 20$ and mostly dendritic trichomes on the upper leaf surfaces, is rarely encountered south of the Canadian border. They assign most collections identified as *D. stenoloba* from the western United States to *D. albertina,* characterized by a chromosome number of $n = 12$ and simple or once-forked adaxial leaf trichomes. My morphological studies of Utah specimens concur that typical *D. stenoloba* is not present in the state, and all collections identified as such represent *D. albertina.* Both taxa belong to Mulligan's (1976) yellow-flowered aneuploid group.

Draba asprella, a species endemic to Arizona and southern Utah, is represented by few herbarium collections and a confusing chromosome literature. A single count of $n = \pm 16$ appears in the primary literature and the Indexes to Plant Chromosome Numbers. This count derives from a population in Coconino Co., AZ studied by Rollins and Rüdenberg (1971), which was not identified to variety in the original paper. Rollins (1993) attributes this count to var. *asprella* and reports an additional, apparently undocumented count of $n = 16$ for var. *stelligera.* The latter count is critical because it seems to place *D. asprella* in Mulligan's (1976) yellow-flowered euploid assemblage, whereas my count of $n = 15$ (Fig. 2) would suggest an affiliation with his aneuploid group. I am confident of my determination, which is based on at least 40 cells from eight individuals. At this point, I am inclined to discount the undocumented euploid report and assign *D. asprella* to the yellow-flowered aneuploid group. In the upcoming field season, I hope to obtain accurate counts for all four varieties and determine whether var. *stelligera* is truly polymorphic with regard to chromosome number.

The available literature provides two chromosome counts for *Draba cuneifolia.* Rollins and Rüdenberg (1971) report a count of $n = 16$ from Pecos Co., TX. Although not identified to variety, this col-

TABLE 1. CHROMOSOME COUNTS ON *DRABA* FROM UTAH AND VICINITY. Counts differing from previously published reports are marked by an asterisk. Apparent first counts for a taxon are marked by a double asterisk following the relevant name. Letters before collection numbers identify the following collectors: ER = Eric Rickart; RS = R. Douglas Stone; JT = James Therrien; W = Michael Windham; TW = Theresa Windham; MEW = Maria Windham; MKW = Molly Windham. Herbaria housing voucher specimens are identified by upper case abbreviations (based on Holmgren et al. 1990) following the collection numbers.

Draba albertina Greene

| $2n = 24$ | UT | Emery Co. | in South Hughes Canyon on the Wasatch Plateau (T14S, R7E, S30); *W & ER 95-185* (UT) |
| $n = 12$ | UT | Salt Lake Co. | E of Guardsman Pass along State Route 152 in the Wasatch Mts. (T2S, R3E, S25); *W 98-320* (MO, NY, UT) |

Draba asprella Greene var. *stelligera* O.E. Schulz

| $n = 15, 2n = 30*$ | AZ | Coconino Co. | along tributary of Bear Wallow Canyon E of Sedona (T17N, R6E, S10); *W 95-250* (ASU, BRY, COLO, UT, UTC); *W, TW & MKW 98-002* (MO, NY, UT) |

Draba cuneifolia Nutt. ex Torr. & A. Gray var. *cuneifolia*

| $n = 15*$ | AZ | Yavapai Co. | WNW of Sedona on the SW side of Fay Canyon (T18N, R5E, S30); *W, JT & MEW 97-005* (MO, UT) |
| $n = 15*$ | UT | Washington Co. | NE of Pinto on low hills overlooking road to Cedar City (T37S, R15W, S26); *W 99-008* (MO, UT) |

Draba juniperina Dorn**

$n = 11$	UT	Daggett Co.	along Browns Park-Clay Basin road in upper Jesse Ewing Canyon (T2N, R24E, S1); *W 96-152* (MO, NY, UT)
$n = 11$	UT	Daggett Co.	along State Route 44 on N side of Spring Creek (T2N, R20E, S19); *W 99-073* (COLO, MO, UT)
$n = 11$	WY	Sweetwater Co.	just E of Richards Gap at S edge of Red Creek Basin (T12N, R105W, S22); *W 00-012* (ASU, BRY, MO, UT)

Draba kassii Welsh**

| $n = 11$ | UT | Tooele Co. | in Goshute Canyon on E slope of the Deep Creek Range (T10S, R18W, S36); *W 98-211* (ASU, COLO, MO, NY, UT) |

Draba maguirei C.L. Hitchc.** var. *maguirei*

| $n = 16$ | UT | Cache Co. | SE slope of Mt. Magog in the Bear River Range (T14N, R3E); *W95-161* (ARIZ, ASU, BRY, COLO, CPH, DAO, ISTC, MO, NY, OGDF, UC, US, UT, UTC) |

Draba nemorosa L. var. *nemorosa*

| $n = 8$ | UT | Summit Co. | N base of Windy Ridge on NE slope of the Uinta Mts. (T2N, R19E, S24); *W 99-072* (COLO, MO, NY, UT) |

Draba rectifructa C.L. Hitchc.**

| $n = 12$ | UT | Juab Co. | N of Mount Nebo near head of Gibson Creek (T11S, R2E, S19); *W 96-204* (UT) |

Draba sobolifera Rydb.**

| $n = 13$ | UT | Piute Co. | S side of Bullion Canyon in the Tushar Mts. (T28S, R5W, S11); *W & RS 95-201* (ASU, BRY, COLO, MO, NY, OGDF, UT) |

Draba spectabilis Greene var. *spectabilis***

| $n = 10$ | UT | San Juan Co. | SE of Gold Basin in the La Sal Mts. (T27S, R24E, S15); *W95-170* (ASU, BRY, COLO, CPH, MO, NY, OGDF, UT, UTC) *W & ER 97-188* (ISTC, UT) |
| $n = 10$ | UT | San Juan Co. | NW slope of South Peak in the Abajo Mts. (T34S, R22E); *W95-182* (ASU, BRY, COLO, CPH, MO, NY, OGDF, UT, UTC) |

Draba subalpina Goodman & C.L. Hitchc.**

$n = 13$	UT	Garfield Co.	along tributary of Red Canyon on the Paunsaugunt Plateau (T36S, R4½W, S1); *W & MKW 92-037* (COLO, MO, UT); *W 96-036* (DAO)
$n = 13$	UT	Garfield Co.	near headwaters of Coyote Hollow on the Paunsaugunt Plateau (T36S, R4½W, S1); *W 98-129* (MO, NY, UT)
$n = 13$	UT	Iron Co.	NW slope of Blowhard Mtn. on the Markagunt Plateau (T37S, R9W, S15); *W 92-135* (BRY, MO, NY, UT, UTC)
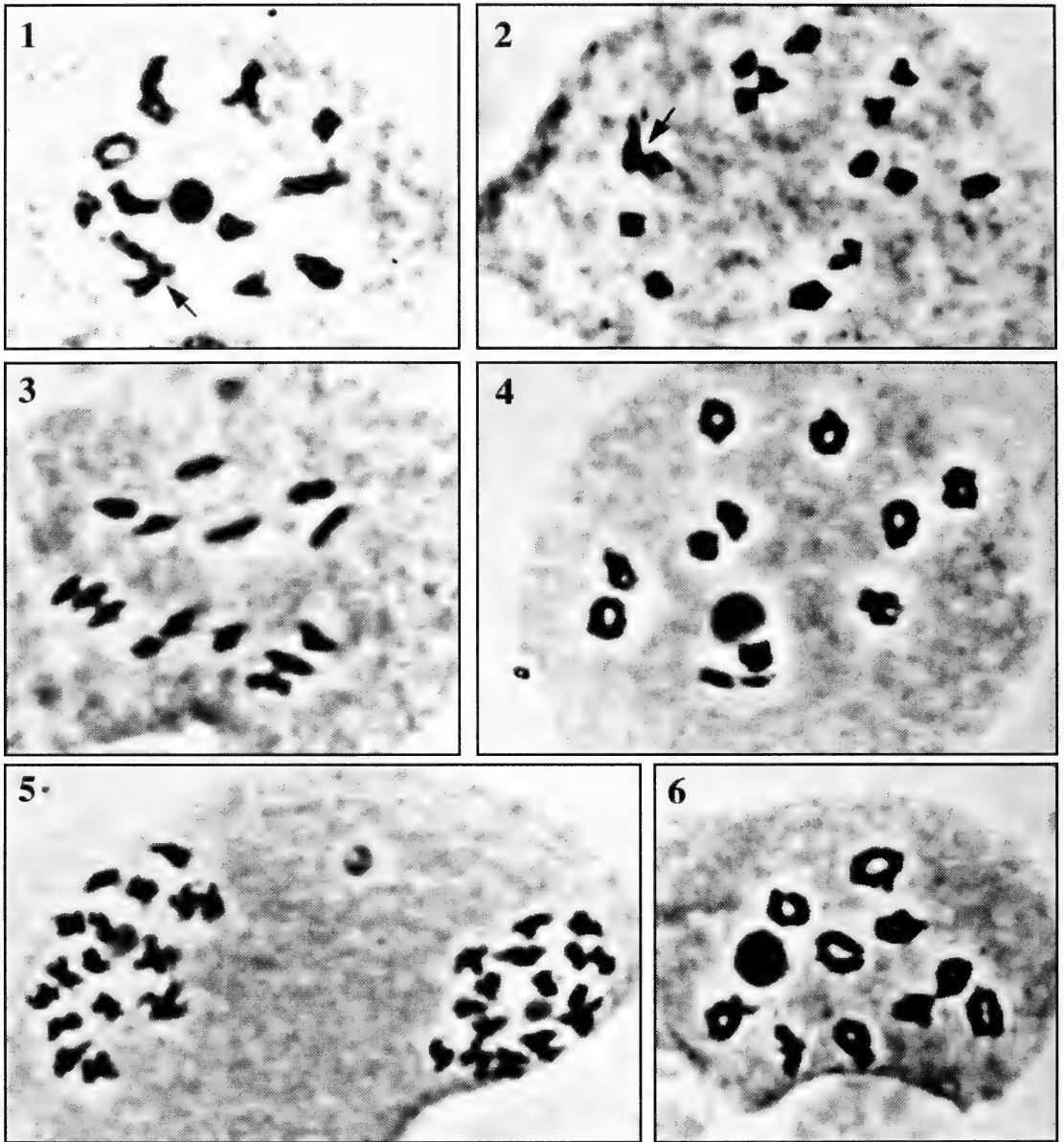
FIGS. 1–6. Meiotic chromosome squashes for various *Draba* species. Solid spherical bodies in Figs. 1, 4, and 6 = nucleoli. Arrows identify overlapping pairs. 1. Diakinesis in *D. albertina* ($n = 12$). 2. Late diakinesis in *D. asprella* var. *stelligera* ($n = 15$). 3. Metaphase I in *D. cuneifolia* var. *cuneifolia* ($n = 15$). 4. Diakinesis in *D. juniperina* ($n = 11$). 5. Late prophase II in *D. maguirei* var. *maguirei* ($n = 16$ at each pole). Faint spherical body near the center of each cluster = nucleolus. 6. Diakinesis in *D. spectabilis* var. *spectabilis* ($n = 10$).

lection is presumed to represent var. *cuneifolia* based on geographic location. Hartman et al. (1975) also report $n = 16$ for a collection of the typical variety from Dallas Co., TX. Given this history, I was surprised to obtain clear preparations of $n = 15$ (Fig. 3) for two populations of *D. cuneifolia* var. *cuneifolia* from Arizona and Utah. These counts were confirmed in at least five cells from three different plants in each population, so it seems likely that the apparent chromosomal polymorphism is

real. It is interesting to note that my counts derive from the northwestern portion of the species distribution, whereas the two reports of $n = 16$ represent the southeastern portion of the native range. Further sampling is needed to determine whether chromosome number truly is correlated with geography in *D. cuneifolia*. Such an investigation also should encompass *Draba reptans*, (Lam.) Fern. which is considered closely related (Hitchcock 1941) or intergradient (Welsh 1993) and apparently displays par-

allel variation in chromosome number (Mulligan 1966; Löve and Löve 1982). Although *D. reptans* is placed in the aneuploid group by Mulligan (1976), the taxon is white-flowered and probably should be assigned to a separate group (Beilstein personal communication).

Draba juniperina is endemic to pinyon-juniper woodlands at the northeastern edge of the Uinta Mountains near "Three Corners", the point where Utah, Wyoming, and Colorado meet. The taxon, long thought to be related to *D. oligosperma* Hook., because of the shared occurrence of doubly pectinate trichomes, has a complex nomenclatural history. It was first separated from the yellow-flowered *D. oligosperma* under the name *D. pectinipila* (Rollins 1953), a taxon typified on white-flowered specimens from alpine habitats in northwestern Wyoming. Dorn (1978) pointed out that the petals of *D. pectinipila* truly are white, but the flowers of populations from southwestern Wyoming and northeastern Utah are yellow when fresh. Additional morphological features were found to correlate with flower color, geography, and habitat, which led Dorn (1978) to describe the Uinta populations as a new species, *D. juniperina.*

Subsequent studies by Lichvar (1983) seemed to reinforce the distinctions among *D. oligosperma, D. pectinipila,* and *D. juniperina* but, in his most recent work, Rollins (1993) abandoned this taxonomy. Stating that designating "deviant types as independent taxa . . . has done little to clarify the nature of the species as a whole" (Rollins 1993), he once again synonymized the segregate taxa under *D. oligosperma.* Kartesz (1994) followed suit, though Welsh (1986a) maintained *juniperina* as a variety of *D. oligosperma* without further comment. There has been little use of this combination, however, because var. *juniperina* is described as having "petals evidently white" (Welsh 1993), a character state not found in Utah specimens.

The chromosome counts presented here for *Draba juniperina* (Fig. 4) provide valuable insight into the taxonomy of this contentious species complex. Studies at two widely separated localities in Daggett Co., UT and one site in Sweetwater Co., WY revealed that *D. juniperina* is a sexually-reproducing taxon with a chromosome number of $n = 11$. This is one of two numbers not previously documented in Mulligan's (1966, 1976) aneuploid series, and clearly establishes this taxon as a member of the yellow-flowered aneuploid group. *Draba oligosperma,* on the other hand, is an apomictic taxon (Mulligan and Findlay 1970) with three reported chromosome numbers: 1) $2n = 32$ from Alberta (Chinnappa and Chmielewski 1987), 2) $2n = \pm60$ from Wyoming (Rollins 1966), and 3) $2n = 64$ from seven populations in Alberta and one in Yukon Territory (Mulligan 1972). These numbers indicate that *D. oligosperma* belongs to Mulligan's (1976) yellow-flowered euploid group.

The difference in chromosome base numbers between *D. oligosperma* ($x = 8$) and *D. juniperina* ($x = 11$) is not trivial. The former is not a simple polyploid derivative of the latter and, if Mulligan (1976) is right in his assessment of relationships, they may belong to different major lineages. The two taxa are easily distinguished using the characters listed by Dorn (1978) and Lichvar (1983), even where their ranges overlap. Even if they grew together, which they apparently do not, there would be no opportunity for hybridization because *D. oligosperma* is apomictic and apparently does not produce functional gametes (Mulligan and Findlay 1970). All of this provides a strong argument for maintaining *Draba juniperina* as a distinct species.

Draba kassii is a very rare species endemic to a few canyons in the Deep Creek Mountains of western Utah. Its relationships are obscure, with Rollins (1993) stating that it "is not closely enough related to any known species of *Draba* to allow inferences as to its phylogeny." Comparisons have been drawn to *D. asprella* (Welsh 1986b) and *D. standleyi* J. F. Macbr. & Payson (Rollins 1993), though both authors suggest that the similarities may be superficial. Chromosome numbers have the potential to play a crucial role in determining the relationships of this species. At least 20 cells from five different plants clearly establish that the chromosome number of *D. kassii* is $n = 11$ (Table 1). This number, which establishes the taxon as a member of Mulligan's yellow-flowered aneuploid group, would seem to rule out a direct phylogenetic link to *D. asprella* ($n = 15, 16?$). The possibility of a relationship to *D. juniperina,* the only other species known to have $n = 11$, is intriguing. However, the two taxa do not appear closely related morphologically, and any hypothesis of relationships will remain speculative until additional *Draba* species (including *D. standleyi*) have been sampled chromosomally.

The phylogenetic affinities of *Draba maguirei* are as contentious as those of *D. kassii,* and it appears that no recent author has ventured to discuss its possible relationships. On first describing the species, Hitchcock (1941) stated that it "is very striking and quite unlike any of the other Drabas from its immediate vicinity. Its closest relatives are probably those of the *ventosa* group . . .". Of the eight taxa comprising Hitchcock's *ventosa* group, chromosome counts have been published for two (*D. ventosa* Gray and *D. ruaxes* Payson & St. John) and a third (*D. sobolifera*) is reported here. All three belong to Mulligan's (1976) yellow-flowered aneuploid group with chromosome numbers based on $x = 12$ and 13. Thus, it is surprising to find that *D. maguirei* var. *maguirei* shows a euploid count of $n = 16$ (Fig. 5). Additional chromosome counts on *D. maguirei* and other members of Hitchcock's *ventosa* group are needed to resolve this apparent conflict.

Draba nemorosa L., a species of widespread occurrence in both North America and Eurasia, was

assigned by Mulligan (1976) to his yellow-flowered euploid group. All populations analyzed chromosomally have shown $n = 8$, regardless of geographic origin. In North America, there have been four counts from Alberta (Packer 1964; Mulligan 1966, 1975), one from Manitoba (Löve and Löve 1982), two from Ontario (Mulligan 1975), and two from Saskatchewan (Mulligan 1966, 1975). It appears that my determination of $n = 8$ (Table 1) from Daggett Co., UT is the first report for the United States. None of the previous North American reports specify variety, though most are surely var. *nemorosa,* the taxon to which my count is assigned following the taxonomy of Kartesz (1994). Although the glabrous-fruited form (var. *leiocarpa*) is considered taxonomically insignificant by many authors, there does appear to be some geographic integrity to its occurrence. Therefore, it seems wise to maintain the distinction until North American populations are studied adequately.

Although Hitchcock (1941) considers *Draba rectifructa* to be a close relative of euploid *D. nemorosa,* little evidence is cited to support such an association. Instead, it appears to be very closely related to *D. albertina,* distinguished from that species mainly by its pubescent upper stems and pedicels. Ongoing studies of populations in northern Utah suggest that *D. rectifructa* and *D. albertina* hybridize when growing in close proximity. Thus, it is not surprising to find that *D. rectifructa* has a chromosome number of $n = 12$ (Table 1), identical to that of its putative aneuploid relative.

Draba sobolifera, endemic to the Tushar Mountains of southern Utah, is considered a member of Hitchcock's (1941) *ventosa* group with close affinities to *D. cusickii* Robinson & D. E. Schulz (Rollins 1993). The chromosome number of the latter species is unknown, but the two members of the *ventosa* complex previously reported, *D. ventosa* and *D. ruaxes,* show $2n = 36$ and $2n = 72$ (Mulligan 1971). They are considered to be triploid and hexaploid respectively, with a base number of $x = 12$. Cytological studies on a population of *D. sobolifera* from Piute Co., UT reveal that it is a sexually-reproducing taxon with a chromosome number of $n = 13$. This is the last number to be documented in Mulligan's (1966, 1976) aneuploid series, and it firmly establishes this species as a member of the yellow-flowered aneuploid group.

There are three previous chromosome counts for *Draba spectabilis,* all from Colorado and all assigned to var. *oxyloba* (Greene) Gilg. & O. E. Schulz by Price (1980). The earliest report (Mulligan 1966) of $n = 10$ seemed to indicate that the species belonged in the aneuploid group. However, two subsequent counts of $n = 16$ and $n = 16 \pm 2$ by Price (1980) suggest an affinity to the yellow-flowered euploid assemblage. My determinations, apparently the first for var. *spectabilis,* are from two widely separated populations in San Juan Co., UT (Fig. 6). They agree with Mulligan's (1966) report of $n = 10$ and point out the need for further sampling to determine the relationships and proper taxonomy of *D. spectabilis.*

Draba subalpina generally is restricted to a single geologic stratum, the Claron Formation of Bryce Canyon National Park and vicinity. Although recent authors have said little regarding its probable relationships, Hitchcock (1941) states that its closest relative is *D. oreibata* J. F. Macbr. & Payson, a species under which it was subsumed prior to 1932. The latter taxon is endemic to central Idaho in its typical form, is similarly white-flowered, and shows a chromosome number of $n = 16$ (Henderson et al. 1980). In light of its proposed relationships and the assumption that *D. subalpina* was a member of the white-flowered euploid group, the actual chromosome number was unexpected. Based on at least ten cells from five individuals in each of three populations, the chromosome count of *Draba subalpina* proves to be $n = 13$ (Table 1). Whether *D. subalpina* belongs to a relatively rare, white-flowered aneuploid group or is more closely related to some of its yellow-flowered congeners remains to be determined. The close proximity (ca. 60 km) of *D. sobolifera,* the only other species known to exhibit $n = 13$, raises intriguing possibilities regarding the relationships of white- and yellow-flowered aneuploids in *Draba.*

Even with the small sample size of this nascent effort, it is clear that the taxonomic composition of the Intermountain *Draba* flora is quite different from the intensively studied assemblage of Canada and Alaska. In the latter, Mulligan (1976) assigned 17 species to his white-flowered euploid group, nine to the yellow-flowered euploid assemblage, and 13 to his yellow-flowered aneuploid group. In my sample from Utah, Wyoming, and Arizona, white-flowered euploids are not represented (unless *D. cuneifolia* belongs here) and yellow-flowered euploids are rare, comprising only *D. nemorosa* and possibly *D. maguirei.* Seven of the Intermountain taxa belong to the yellow-flowered aneuploid assemblage and the remaining taxon (*D. subalpina*) is a white-flowered aneuploid of uncertain affinity.

A growing number of chromosome counts for the region suggests that the Intermountain West may be a center of diversity for aneuploid *Draba.* With the discovery of both $n = 11$ and $n = 13$ among local endemics, a complete series of base numbers extending from 8 to 16 has been documented. Only $n = 9$ and $n = 14$ are missing from my sample, and those numbers have been confirmed in other taxa from the region. This means that every major step in the process of aneuploid evolution is preserved among the *Draba* species of the Intermountain West. In this assemblage of *Draba* species, we have an unprecedented opportunity to study the processes of chromosomal evolution and speciation in plants. With further cytological sampling and concurrent DNA studies of the group, we soon may be in a position to elucidate the evo-

lutionary history of this interesting and diverse set of organisms.

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A FLORISTIC STUDY OF TSEGI CANYON, ARIZONA

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ABSTRACT

The purpose of this study is to list the vascular flora present in Tsegi Canyon, Arizona, and to describe any change in flora that may have happened during the past hundred years. Plants were collected during the years 1994–1997. Three hundred and ten species representing seventy three families are reported to occur within the Tsegi drainage. Three percent of these species are endemic to the Colorado Plateau and twelve percent of the species found are non-native. A change in floristic composition is found to have occurred in the last century, correlated with a shift in habitat types in the canyon. The canyon of the late 1800's had a slowly moving stream and marshes along a continuous alluvium. The present canyon has a faster moving stream that has eroded much of the alluvium to bedrock. One species, *Cymopterus beckii* is a new report for Arizona and also is listed as a candidate for rare and endangered species status.

Floristics on the Colorado Plateau have not been widely studied, with perhaps the exception of the Grand Canyon (Phillips et al. 1987). The reason for this may be the remoteness of the area from civilization and difficulty in traveling to many parts of the plateau due to lack of roads and extremes in temperature. Although most of the plateau vegetation consists of pinion and juniper in higher elevations and desert scrub in the lower, there are also canyons which harbor a very different flora, including some relict populations, as well as seeps and alcoves with their unique flora. The purpose of this paper is to describe one of the canyons on the plateau that includes year-round, running water as a small stream, as well as seeps and alcoves.

Although this is the first compilation of flora done of Tsegi Canyon, the flora has been studied and described by various researchers previously. One of the first descriptions of the flora of the canyon was done by Clute (1920). J. T. Hack (1945) also studied the canyon as part of his documentation of the erosion/deposition cycles in northern Arizona. He, along with Dean (1969) and Weatherill (1953) describe the erosion of this area that occurred within the last hundred years, which could possibly be related to the environmental changes that occurred in the southwest during the first part of the century (Hastings & Turner, 1965). An inventory was done for the park service in the 1970's, with Brotherson et al. (1978) publishing a flora of Navajo National Monument. Historical collections were examined at the Walter B. McDougall Herbarium, the Deaver Herbarium, the U. of A. Herbarium, and at the herbarium at Navajo National Monument.

Study area description. The Tsegi Canyon drainage system is a complex of canyons that forms the headwaters of Laguna Creek, one water supply for the town of Kayenta, AZ. Tsegi Canyon, whose name in the Navajo language means 'in the rocks' or canyon, is in Navajo County in the northeast

corner of Arizona, 540000E, 4054000N, 36°40′N, 110°30′W. Tsegi Canyon includes in its boundaries two of the three sections of Navajo National Monument, Betatakin and Keet Seel.

The head of Tsegi Canyon is located on the Organ Rock Monocline. This is an uplift that is followed by Highway 160, in Long Valley between the Shonto Plateau and Black Mesa. The canyon is a complex drainage cut into the Shonto Plateau on the east and Skeleton Mesa to the west. Six different geological formations are visible in the canyon. The top of the plateau is made of Navajo Sandstone, the formation responsible for the magnificent sandstone cliffs at the top of the canyon. This layer is of Jurassic age and made of wind-blown sand and dunes. The layer just under the Navajo Sandstone is the Kayenta formation consisting of gray-red sandstone and some clay shale. This layer is about 61 meters thick at the head of the canyon. Because the Navajo sandstone is porous, it allows percolation of water onto the top of the less porous Kayenta formation. The water moves laterally over the Kayenta formation to flow out and form seeps on the canyon walls. Exfoliation of the sandstone above the seeps causes the formation of the alcoves that were utilized by the Anasazi. The layers under the Kayenta formation are a part of the Glen Canyon group. In the canyon, it is represented by the Lukachukai member of the Wingate sandstone. This is a reddish-brown, cliff-forming sandstone often responsible for the rockfall in the canyon. Under this is the Chinle formation. It is represented by two strata, the Churchrock member and the Owlrock member. The Churchrock member consists of brownish-red siltstone, mudstone, and fine-grained sandstone with small, white spots and streaks. Below is the Owlrock member which consists of reddish-brown siltstone and mudstone, and greenish-gray claystone laid down in the Triassic Age. There is also a limited exposure located north of the Tsegi Hotel, of Petrified Forest member with red, purple, and green/gray betonite claystone. On

the bottom of the canyon is alluvial fill (Beaumont & Dixon 1964).

There are three layers of alluvial deposition in Tsegi Canyon. The oldest layer is the Jeddito formation that was laid down before 3500 BC. This is overlaid by the Tsegi formation that was laid down between 3500 BC and AD 1300. The youngest layer of alluvium is the Naha formation that was laid down between 1450 and 1880 (Hack 1945). Although there is a small amount of post-1900 alluvium, at the present there is more erosion happening than deposition. The reasons for the deposition and erosion cycles is not definitely known. It has been suggested that rainfall, climate fluctuations, and land management practices may all be contributors to this cycle, with perhaps, the climate being the most influential factor (Clay-Poole 1989). However there is also evidence that human activity has affected arroyo cutting in the canyon. The cutting of the Tsegi-Naha arroyo in Keet Seel was preceded by the clearing of an aspen forest at the bottom of the canyon in the 1200's. After the abandonment of Keep Seel, the area was redeposited with alluvium and recolonized by *Quercus gambelii* (Dean 1969). However, with the new arroyo cutting of the present century, the distribution of oaks have retreated to the upper side alluvium.

The climate at Tsegi Canyon is arid with cold winters and hot summers. The daily average temperature at Tsegi is Celsius. Temperatures vary from highs of 340 to 380° C in July to lows of −230 to 130° C in the winter. The frost-free season averages about 155 days. Precipitation in the canyon is variable from year to year. Over a 17-year span, the rainfall at the Betatakin Monument ranged from a low to 17.3 centimeters to a high of 47.7 centimeters (U.S.D.C. 1979–1996). The variability is caused by differences in winter precipitation and is also enhanced by the fact that monsoon rains are very spotty and usually do not equally wet all parts of the canyon (Dean 1969).

METHODS

Seventeen collecting trips to Tsegi Canyon were made between 1994 and 1997. The main focus of collecting was to include as many species as possible for the floristic list. The collections were done between the months of April and October, as most of the vascular flora is dormant during the winter. Lower Tsegi Canyon was visited April 23, 1994; May 30, 1994; July 16, 1994; and August 12, 1994. Wildcat Canyon and Lone Cottonwood Canyon were visited June 19, 1995, July 26, 1995, and August 11, 1995. Upper Tsegi Canyon, Fir and Betatakin Canyon were visited June 3, 1994; August 7, 1994; September 16, 1994; May 21, 1995; May 29, 1996; and August 8, 1996. Dowozhiebito and Keet Seel Canyons were visited June 18, 1994; May 5, 1996; September 28, 1996; and June 26, 1997. Four of the trips, May 29, 1996; August 8, 1996; Sep-

tember 28, 1996; and June 26, 1997 were made at the request of the National Park Service as a survey for rare and endangered species. At this time, collections were made at Betatakin National Monument and Keet Seel National Monument. However, the majority of the collecting was done on Navajo Tribal land.

All specimens were pressed, dried, and stored at the Deaver Herbarium (ASC) at Northern Arizona University, with duplicates sent to the Navajo Tribal Heritage Herbarium. Specimens were named following Kartesz (1994). Previous collections located at the Deaver Herbarium (ASC), the museum of Northern Arizona Herbarium (MNA), and the University of Arizona Herbarium (ARIZ) were used for comparison.

A classification model, modified from Rowlands' Colorado Plateau Vegetation Assessment and Classification Manual was used to describe the various vegetation assemblages in the canyon. I determined dominant/co-dominants by using the largest sized plants that appeared to be the most abundant (Bonham 1989; Rowlands 1994). The other notable species are included to help describe the assemblages. Boundaries were determined using physical boundaries, such as terrace levels and natural altitudinal separations. The assemblages were mapped out using USGS topographic maps of the Betatakin, Keet Seel, and Marsh Pass quadrangles with additional information relating to location and size taken from aerial photos. The maps were drawn by hand and the areas of the vegetation assemblages determined using a Mackintosh scanner and NIH Image area analysis.

RESULTS

There were 310 species found in Tsegi Canyon during the study years. In comparison, 518 species were found in Canyon deChelly National Monument (Halse 1973; Harlan 1976), 293 species were found at Navajo National Monument (Brotherson 1978), 376 species were found in Volunteer and Sycamore Canyon (Shilling 1980), and 326 species were found in the Walnut Canyon National Monument (Arnberger 1947; Spangle 1953; Joyce 1976). There are eight vegetation assemblages described in this study for Tsegi Canyon which include the *Pseudotsuga* assemblage, *Populus tremuliodes* assemblage, the *Pinus edulis/Juniperus osteosperma* assemblage, *Quercus gambelii* assemblage, *Atriplex/Artemisia* assemblage, the *Juncus* marshland assemblage, *Betula occidentalis* assemblage, the *Gutierrezia* assemblage, and the *Pucinnellia* badlands assemblage. This classification is split into more detail than the USFS digitized classification system (Brown 1980) and some of the assemblages are combined compared to Rowlands (1994). Because there is no standardized way to classify the complex systems of a riparian canyon on the Colorado Plateau, this scheme was created based on both classification systems.

Pseudotsuga occurred in shaded, mostly north and west facing areas in the side canyons of Tsegi. This assemblage consists of about 8% of the total coverage of vegetation sampled in the canyon. Most *Pseudotsuga menziesii* individuals encountered were older trees. A study of whether or not seedlings are present in high enough numbers to replace older trees would be of value for this area. The *Pseudotsuga* often graded down into populations of *Populus tremuliodes* in the moist side canyons, and sometimes an individual fir could be found in the upper regions of a stream bed. Rarely, *Pinus ponderosa* could be found growing among the firs. In the upper Keet Seel canyon, few individuals of *Abies concolor* were found among the fir. Shrubs growing in this assemblage include *Ssymphoricarpos oreophilius*, *Ribes cereum*, *Ribes inerme*, and *Amelanchier alnifolia*. Herbaceous plants include *Antennaria parvifolia*, *Mahonia repens*, *Corydalis aurea*, *Galium aparine*, and *Valeriana acutiloba*. This assemblage is included in the Cold Temperate Forest and Woodlands, Rocky Mountain Montane Conifer Forest, Douglas fir-White Fir series, 122.311. *Pseudotsuga menziesii* Association in the Digitized Systematic Classification used by the Forest Service (Brown 1980). In Rowlands (1994), this is part of the Montane Zone, Forest and Woodland Formation, and *Pseudotsuga menziesii* Series.

Populus tremuloides creek bottoms include plants adapted to a shady, moist environment. *Populus tremuloides* covers less than 1% of the area studied, occurring in the upper areas of the Betatakin-Fir Canyon side canyons. This assemblage is bounded above mostly by *Pseudotsuga menziesii* on the shady sides of the canyons and *Quercus gambelii* on the more sunny sides. *Betula occidentalis* can be found further down the creek bed if there is running water, otherwise it usually ends abruptly in *Pinus/Juniperus* or sandy creek bottom vegetation. Other trees that can be found in this assemblage include *Pseudotsuga menziesii* and *Prunus virginiana*. Shrubs present include *Rhus aromatica*, *Symphoricarpos oreophilus*, *Cornus sericea*, *Arctostaphylos pungens*, *Ribes leptanthum*, *Rosa woodsii*, *Salix exigua*, and *Salix lasiolepis*. Herbaceous plants include *Equisetum arvense*, *Carex athostachya*, *Eleocharis palustris*, *Juncus arcticus*, *Fritillaria atropurpurea*, *Smilacina stellata*, *Poa praatensis*, *Erigeron speciosus*, *Silene menziesii*, *Lathyrus brachycalyz*, *Androsace septentrionalis*, *Clematis ligusticfolia*, *Thalictrum fendleri*, *Heuchera parvifolia*, and *Mimulus rubellus*. The closest classification of this assemblage found in the USFS classification is the Great Basin Interior Strand, which is very non-specific (Brown 1980). Rowlands (1994) has a *Populus tremuloides* Series in his Forest and Woodlands Formation. However, I do not feel that this quite fits as it describes aspen in a pine forest where the pines will eventually succeed the aspen. Here the aspen are the climax species, with aspen saplings replacing older trees.

The most common assemblage found on the Shonto Plateau is the *Pinus edulis/Juniperus osteosperma*. This assemblage forms 50% of the plant communities mapped. In the canyon, this assemblage is found in many of the upper ledges and south facing canyon sides. This assemblage surrounds the Monument headquarters and is common on the top of Skeleton Mesa. Shrubs that can be found in association with this assemblage include *Ephedra viridis*, *Chrysothamnus nauseosus*, *Shepherdia rotundifolia*, *Fendleera rupicola*, *Amelanchier utahensis*, *Cercocarpus intricatus*, *Cerccocarpus montanus*, *Holodiscus dumosus*, and *Yucca angustissima*. Herbaceous plants include *Allium macropetalum*, *Calochortus aureus*, *Bouteloua gracilis*, *Cymopterus acaulis*, *Artemisia dracunculus*, *Psilostrophe sparsiflora*, *Heterotheca villosa*, *Arabis perennans*, *Streptanthus cordatus*, *Echinocereus triglochidiatus*, *Opuntia polycantha*, *Astragalus ceramicus*, *Mirabilis multiflora*, *Ipomopsis aggregata*, *Castilleja linariifolia*, *Cordylanthus wrightii*, and the parasitic *Phoradendron juniperinum*. The *Pinus edulis/Juniperus osteospermus* assemblage is part of the Forest and Woodland Formation (Rowlands 1994) and classified by the USFS as part of the Great Basin Conifer Woodland, Pinion-Juniper Series (Brown 1980).

The area described as the *Quercus gambelii* assemblage occurs on the upper terraces in side canyons draining from west to east, though there are exceptions in the upper areas included in this study. This assemblage is estimated to cover about 2% of the study area. The main component of this assemblage are thickets of *Quercus gambelii* with occasional larger trees of *Quercus* included. This area's shading consists of thick leaf litter and generally is not as diverse as the more expansive *Pinus/Juniperus* assemblage. Many plants found here grow in spaces in the thicket where more light can penetrate. Other shrubs included in this assemblage are *Ribes cereum* and *Prunus virginiana*. The herbaceous cover includes *Juncus arcticus*, *Smilacinia stellata*, *Bouteloua curtipendula*, *Opuntia phaeacantha*, *Erigeron utahensis*, and *Lathyrus brachycalyx*. Rowlands (1994) classifies this as the Tall Shrubland Formation, *Quercus gambilii* Series. The USFS Digitized Classification (Brown 1980) includes this in the Cold Temperate Scrublands, Great Basin Montane Scrub, Oak-Scrub Series.

The *Atriplex/Artemisia* assemblage dominate on the lower terraces above the main creek and at the mouths of the side canyons. This is the second largest vegetation assemblage covering about 22% of the total canyon. Although there may be an occasional Pinion or Juniper tree associated with this assemblage, the dominant larger plants are the shrubs *Atriplex canescens* and *Artemisia tridentata*. There are also occasional lone *Elaegnus angustifolia* individuals of unknown origin, possibly planted by members of the family that use the canyon (Melberg 1988), or distributed by birds. There is also a small stand of about four *Ulmus pumila* at

one site, planted along the side of the dirt road. Shrubs associated with this area include *chrysothamnus viscidiflorus, Sarcobatus vermiculaatus, Poliomintha incana,* and *Cercocarpus intricatus.* Herbaceous plants include *Elymus smithii, Artemisia frigida, Helianthus peetiolaris, Senecio multilobatus, Cryptantha crassisepala, Descurainia pinnata, Salsola iberica, Astragalus amphioxys, Phacelia ivesiana, Spaeralcea parvifolia, Mirabilis oxybaphoides, Gayophytum racemosum, Orobanche multiflora, Erigonum cernuum, Ranunculus testiculatus,* and *Verbeena bracteata.* Rowlands (1994) split these two shrub species into two separate series in his classification scheme. However, in Tsegi Canyon, the two species were found in many places together, and thus would be hard to separate into separate assemblages. The closest classification found in the USFS classification manual (Brown 1980) is defined as the Cold Temperate Desertlands, Great Basin Desertscrub, Mixed Scrub Series.

The *Juncus* marshland assemblages were usually found at the bottoms of most small side creek drainages and flattened areas below seeps. The *Juncus* assemblage is a minor component of the canyon, consisting of less than 1% of the canyon surveyed. These areas were often heavily used by cattle and damaged by trampling. This assemblage had only occasional *Elaeagnus angustifolia* or *Tamarix ramosissima.* There was also one example of a *Populus fremonti* tree at the edge of one marshland. Herbs found in this assemblage include *Juncus arcticus, Equisetum arvense, Polypogon monspeliensis, Scirpus pungens, Aster frondosus, Conyza canadensis, Taraxacum officinale, Crypthantha inaequata, Lepidium virginicum, Epilobium ciliatum, Plantago major,* and *Ranunculus cymbalaria.* Rowlands (1994) classifies this as a Marshland Formation, *Juncus arcticus* Series. Using the USFS classification this assemblage would be included in the Cold Temperate Marshlands, Great Basin Interior Marshland, Rush Series (Brown 1980).

Betula occidentalis creek bottom assemblage was found only in the areas of Betatakin-Fir Canyon drainages and some north-draining side canyons of Keet Seel and upper Dowozhiebito Canyon. This assemblage accounted for about 1% of the area mapped. In the Betatakin area it was bounded above by *Populus tremuoides* and below by *Elaeagnus angustifolia.* In other side-canyons, *Betula* was the uppermost tree species on the drainage floor. The *Betula* commonly grew along both sides of drainages that included year-round running water. Another tree species associated with this assemblage was *Acer negundo. Salix monticola* and *S. lasiolepis* were also found growing among the birches. Herbaceous plants found in this assemblage include *Corallorhiza maculata, Toxicodendron rydbergii,* and *Chenopodium album.* Like the *Quercus* assemblage, the density of the trees tend to shade the floor of the creek. This, along with occasional high water levels, tend to limit the num-

ber of herbs present. Rowlands (1994) classifies this in the Montane Zone, Tall Shrubland Formation, *Betula occidentalis* series. However, this would be more applicable if it was placed in a riparian formation, which is not included in this classification scheme. In the USFS (Brown 1980) there is a Cold Temperate, Great Basin Interior Strand, which includes all riparian vegetation in the Great Basin Biome.

The bottoms of the major drainages are classified as the *Gutierrezia* stream bottom assemblage. This assemblage covers about 18% of the canyon. The soils in this area are characterized by sandy deposits that are typically scoured at least once a year by flooding. There is also quicksand after floods and other areas that are devoid of vegetation because of animal or human (automobile) use. This assemblage also includes areas of bare sandstone and low, dry, sandy dunes. Shrubs that grow here include *Gutierrezia sarothrae, Chrysothamnus depressus,* and *Artemisia frigida.* Herb species that grow here include *Equisetum hyemale, Chenopodium leptophyllum, Salsola iberica, Astragalus amphioxys, Nama retrorsum, Tripterocalyx micranthus, Oenothera pallida,* and *Verbascum thapsus.* Rowlands (1994) has a *Gutierrezia sarothrae* series in his classification under the Low Shrubland Formation. The USFS (Brown 1980) includes this area under the Great Basin Interior Strand.

Downstream the *Betula* individuals in the Betatakin drainage is a stand of *Elaeagnus angustifolia.* Here, *E. angustifolia* is growing along both sides of the creek. Whether *E. angustifolia* is displacing the birch or growing in an area that is for some reason too low in the drainage for the birch is unknown. However, since *E. angustifolia* is an introduced species, and there is an area of interface between the two species, and because the Elaeagnus seems to be spreading in the canyon (Melberg, 1994), the former possibility needs to be examined. Elsewhere in the canyon, *E. angustifolia* is mostly present as individual trees or young plants. Young plants were found growing in the Keet Seel drainage, about seven miles from Betatakin, and other young plants were found in side canyons across and above the Betatakin drainage. This is one species that needs to be watched closely because it seems to be able to colonize some local areas and possibly out-compete native growth.

The *Puccinellia* assemblage consists of few plant species growing on betonite clays. This assemblage covers less than 1% of the area mapped. The largest example of this assemblage is in upper Wildcat Canyon on the north-west facing side of the canyon. Most of the plants are concentrated near a small seep. The area grades into the *Pinus/Juniperus* assemblage above it on the canyon sides. Plants included here are *Apocynum cannabinum* and *Puccinellia distans.* The closest classification in Rowlands (1994) would probably be the Submontane Barren Formation 1408.03. In the USFS

TABLE 1. A COMPARISON OF THE TEN LARGEST FAMILIES OF VASCULAR FLORA OF TSEGI CANYON, PETRIFIED FOREST, N.P., CAPITOL REEF N.P., GRAND CANYON N.P., AND THE NAVAJO NATION. *Family not in top ten % flora, [1]Kierstead, 1981, [2]Heil et al., 1993, [3]Phillips et. al., 1987, [4]Mayes and Rominger, 1994.

Family	Tsegi Canyon	Petrified[1] Forest N.P.	Capital[2] Reef N.P.	Grand[3] Canyon N.P.	Navajo[4] Nation
Asteraceae	19.0	19.9	20.4	16.6	17.6
Poaceae	11.2	19.6	14.0	11.3	11.7
Brassicaceae	5.5	4.7	6.3	4.6	4.9
Fabaceae	5.2	5.6	8.4	4.8	8.1
Scrophulariacea	3.3	*	3.5	3.1	3.3
Chenopodiaceae	3.5	6.8	3.9	*	3.1
Rosaceae	3.2	*	*	2.3	2.5
Boraginaceae	2.9	*	*	3.0	2.3
Cactaceae	2.5	*	*	*	*
Salicaceae	2.2	*	*	*	*
Total in Top Ten % of Flora	58.5%	72.4%	68.8%	53.6%	59.9%

classification is it closest to the Cold Temperate Grasslands under the Great Basin Shrub-Grasslands (Brown, 1980).

Alcoves, hanging gardens, and seeps are very specialized and variable components of the canyon. These plant communities vary according to directional aspect, amount of sunlight received, depth of alcove, soil type, and amount and duration of water flow. Alcoves at Tsegi are created out of sandstone eroded by vertical movement of water across rock seams. Alcoves range from less than a meter to many meters in size, and may also include prehistoric housing ruins. The species most common to alcove seeps include *Mimulus eastwoodiae* and *Adiantum capillus-veneris*. Other species found in cave seeps include *Mentha arvensis, Selaginella mutica, Platanthera zothecina, Pragmites australis, Carex aurea, Carex lanuginosa, Carex specuicola, Oenotheera elata, Aquilegia micrantha, Epipactis gigantea*, and *Mimulus guttatus*. Another type of seep found in the canyon comes out of a vertical canyon side, usually in loose, sandy soil.

This type of seep receives a greater amount of sunlight in comparison to the hanging gardens in the alcoves. The plant composition in this type of seep includes grasses such as *Avena fatua, Elymus canadensis, Elymus elymoides, Glyceria striata, Hordeum jubatum, Poa annua, Polypogon monspeliensis, Schizachyrium scoparium, Secale cereale*, and *Sphenooopholis obtusata*. Other plants at these sites include *Cymopterus beckii, Apocynum cannabinum, Artemisia ludoviciana, Aster frondosus, Solidago sparsiflora, Lithospermum incisum,* and *Glycyrrhiza lepidota*. There is not a dominant species listed because of the differences of plant components present among various seeps. Seeps and alcoves in this area can harbor endemic, rare, and endangered plant species, such as *Carex specuicola* and *Platanthera zothecina*.

DISCUSSION

The floristic composition of representative plant families of the canyon is similar to the floristic composition of the Navajo Nation as last reported by Mayes and Rominger (1994; Table 1). The canyon has a similar number of *Asteraceae* and *Poaceae* when compared to other similar sites. This is surprising as Tsegi, and the Navajo Nation, are grazed while the national parks used for comparison are not. Perhaps a more detailed study is needed to determine whether or not the grazing affects floristic composition. The differences in the families showing a small percentage of the total probably can be accounted for by the concentration of specialized habitat types, such as alcoves and elevation at each site.

Species considered endemic to the Colorado Plateau by Welsh (1993) include *Calochortus aureus, Platanthera zothecina, Astragalus zionis, Astragalus cottamii, Astragalus sesquiflorus,* and *Cymopterus beckii*. The rare and endangered plants include *Platanthera zothecina*, a candidate species, *Carex specuicola*, a listed threatened plant, and *Nama retrosum, Penstemon pseudoputus, Astragalus cottami,* and *Cymopterus beckii*, whose populations are being watched. *Aletes sessiliflorus*, identified by L. Constance, and *Cymopterus beckii* were new reports for the state of Arizona.

Introduced species are listed in Table 2. These exotic plants species comprise about 10% of the total plant population of the canyon. Many of the weedy herbs may have been introduced by domestic grazing animals, whose feed is supplemented with commercial hay, and also by the disturbing of the land by off-road vehicles. Three introduced plants, *Tamarix ramosissima, Elaeagnus angustifolia,* and *Ulmus pumila* were introduced purposely in the Southwest as shade trees and to aid in erosion control (Welsh 1993). Of these, *E. angustifolia* is considered harmful in the canyon by the National Park Service. Attempts are currently being made to keep it out of Betatakin National Monument (Melberg 1996).

There is evidence that suggests that the inner canyon has changed in the last 150 years. In 1916, L.C. Whitehead (MNA) collected *Epipactis gigan-*

TABLE 2. EXOTIC PLANTS FOUND IN TSEGI CANYON. [1]Exotics found in Navajo Monument not listed in Brotherson et. al., 1978. [2]State of Arizona Designated exotic plant species.

Species Name	Common Name	Origin
Monocotyledoneae		
Poaceae		
Avena fatua	Wild Oats	Eurasia
Bromus tectorum	Cheat Grass	Eurasia
Dactylis glomerata	Orchard Grass	Eurasia/Africa
Erenopyrm triticeum	Annual Wheat Grass	Central Asia
Polypogon monospeliensis	Rabbitfoot Grass	Eurasia/Africa
Polypogon semiverticillatus	Water Polypogon	Eurasia
Secale cereale	Cultivated Rye	Eurasia
Dicotyledoneae		
Asteraceae		
Artemisia absinthium	Absinthe	Europe
Cirsium vulgare	Bull Thistle	Eurasia
Latuca serriola	Prickly Lettuce	Europe
Sonchus asper	Spiny Sow Thistle	Europe
Tagetes patula	Marigold	Mexico
Taraxacum officinale	Dandelion	Eurasia
Tragopogon dubius[1]		Eurasia
Xanthium strumarium	Cocklebur	Eastern U.S.
Brassicaceae		
Capsella bursa-pastoris	Shepherds Purse	Europe
Corisppora tenella[1]	Musk mustard	Asia
Descurainia sophia		Europe
Sisymbrium altissimum	Tumble Mustard	Europe
Chenopodiaceae		
Kochia scoparia	Summer Cypress	Eurasia
Salsola iberica	Tumble Weed	Asia
Elaegnaceae		
Elaeagnus angustifolia	Russian Olive	Europe
Fabaceae		
Trifolium repends[1]	White Clover	Europe
Medicago lupulina	Hop Clover	Europe
Medicago staiva	Alfalfa	Europe
Melilotus album	White Sweet Clover	Europe
Geraniaceae		
Erodium cicutarium	Storkbill	Europe
Lamiaceae		
Draccocephalum tymiflorum	Horehound	Eurasia
Marrubium vulgare		Eurasia
Plantaginaceae		
Plantago lanceolata		Eurasia
Plantago major[1]	Broadleaf Plantain	Europe
Ranunculaceae		
Ranunculus testiculatus[1]	Bur Buttercup	Eurasia
Scrophulariaceae		
Verbascum thapsus	Wooly Mullein	Eurasia
Tamaricaceae		
Tamarix ramosissima	Tamarack	Eurasia
Ulmaceae		
Ulmus pumila[1]	Siberian Elm	Asia
Zygophyllaceae		
Tribulus terrestris[2]	Puncture Vine	Eurasia

tea, *Pinus edulis, Abies concolor, Equisetum hiemale, Salix exigua, Populus tremuliodes,* and *Quercus gambelii* from Tsegi Canyon. All of these species are now present in the canyon, though the *Abies* is now only found in one side canyon northeast of the Keet Seel ruin. Of these, *Epipactis, Equisetum, Salix,* and *Populus* are usually found in more mesic soils. Clute (1920) described the canyon as containing desert plants and some mesophytes. He also stated, that at the time, there was a layer of "peat two feet thick" that contained snail shells. He felt that this was evidence of the previously reported lakes and swamps. The most extensive historical collection was done by the Wetherill family in the 1930's. Most of the plants in that collection are also found at the present and are indicated as such in the floristic appendix of this paper. Plants included in the Wetherill collection (Wyman

1951) that were not found in the present study or listed by Brotherson et al. (1978) in their survey of Navajo National Monument include *Abronia fragrans, Cologonia angustifolia, Amaranthus retroflexus, Juniperus communis, Bromus anomalus, Bromus vulgaris, Pachystema myrsinites, Oenothera lavandulifolius, Eriophyllum lanosum, Achillea lanulosa, Setaria viridis, Pedicularis centranthera, Bouteloua eriopoda, Sporobolus pulvinatus,* and *Nicotiana trigonophylla.* These particular plant species could possibly survive in the microhabitats of the present Tsegi drainage. Why they were not found during my survey periods is unknown. Although One Side Canyon was in the past called "Water lily Canyon", I could find no evidence of water lilies collected in the early 1900's.

CONCLUSION

Tsegi Canyon is a complex canyon of numerous drainages. It has experienced a large amount of erosion in the last hundred years. This has changed the nature of the bottom of the canyon from marshy pools to a faster moving creek. Erosion has lowered the bottom of the creek and that lowered the water table and affected small seeps along the sides of the canyon. Some marshy areas still exist, but only in limited areas in protected side-canyons. There is a good possibility that changes in the fauna and flora have occurred along with local extinctions. Hopefully, more studies will be done here to document the flora and fauna in this remote area of Arizona. Information needs to be gathered to create an effective means of preserving this riparian area while still allowing usage by local inhabitants.

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APPENDIX 1

FLORA OF TSEGI CANYON

The nomenclature in this flora follows Kartesz (1980). The letter designation for endemic species is 'A', exotic species is 'B', federal category C2 is 'C2', fegeral category C3 is 'C3', federally listed threatened and endangered is 'T', those included in the Wetherill collection are 'W'.

Selaginellaceae

Selaginella mutica D. C. Eaton. Perennial; moist areas under cave seeps, Apr.–June.

Equisetaceae

Equisetum arvense L. Perennial; sandy, moist areas by springs and seeps, June–Aug.

Equisetum hyemale L. Perennial; sandy, moist area near upper Laguna Creek. June–Aug., W.

Adiantaceae

Adiantum capillus-veneris L. Perennial; cave seeps and hanging gardens, May–Aug. W.

Aspleniaceae

Woodsia oregana D.C. Eaton. Perennial; seep running over crack in sandstone cliff, Sept.

Cupressaceae

Juniperus osteosperma (Torr.) Little. Evergreen Tree; widespread on sandy flats, W.

Ephedraceae

Ephedra viridis Cov. Evergreen shrub; widespread on sandy flats, W.

Pinaceae

Abies concolor (Gord. & Glend.) Lindl. Evergreen tree; shady, upper areas of Keet Seel Canyon.

Pinus edulis Engelm. Evergreen tree; widespread on sandy flats, W.

Pinus ponderosa Dougl. Evergreen tree; sometimes found in side canyons. W.

Pseudotsuga menziesii (Mirbel) Franco. Evergreen tree; found in shady side canyons, W.

Agavaceae

Yucca angustissima Engelm. ex Trel. Perennial; found on sandy flats, flowers in June, W.

Yucca baccata var. baccata Torr. Perennial; north slope of Betatakin canyon, W.

Commelinaceae

Tradescantia occidentalis (Britt.) Smyth. Perennial herb; trail to Betatakin ruins and sandy areas in side canyons, May–June, W.

Cyperaceae

Carex aurea Nutt. Perennial herb; seeps and springs, June–Aug.

Carex lanuginosa Michx. Perennial herb; seep near Keet Seel Ruins, June–Aug.

Carex rossii F. Boott. Perennial herb; Betatakin canyon by trail bench, June–Aug.

Carex specuicola J. T. Howell. Perennial herb; hanging gardens and seeps, June–Aug., A, T.

Eleocharis palustris (L.) R. & S. Perennial herb; Betatakin creek, June–Aug.

Scirpus pungens Vahl. Perennial herb; moist creek bottoms, June–Aug.

Juncaceae

Juncus arcticus Willd. Perennial herb; moist creek bottoms, May–Aug., W.

Juncus bufonius L. Perennial herb; moist sand, lower sidecanyons, June–Aug.

Juncus saximontanus A. Nels. Perennial herb; by small creek, May–June, W.

Liliaceae

Allium macropetalum Rybd. Perennial herb; sandy flats, Apr.–May, W.

Androstephium breviflorum Wats. Perennial herb; trail to Betatakin, Apr.–May. W.

Calochortus aureus Wats. Perennial herb; sandy flats, June–July. W.

Fritillaria atropurpurea Nutt. Perennial herb; creekside, Fir Canyon, June–July W.

Smilacina stellata (L.) Desf. Perennial herb; moist canyon bottoms, June–Aug. W.

Orchidaceae

Corallorhiza maculata Raf. Perennial herb; lower Betatakin canyon, under trees, June–July, W.

Epipacis gigantea Dougl. ex Hook. Perennial herb; hanging gardens and seeps, June–Aug., W.

Platanthera zothecina Higgins & Welsh. Perennial herb; hanging gardens and cave seeps, including Betatakin ruin, July–Aug. A, C2, W.

Poaceae

Agrostis exarata Trin. Perennial herb; beside small stream in Keet Seel Canyon, June.

Arista purpurea Nutt. Perennial herb, dry sandy soil, May–June, W.

Avena fatua L. Annual herb; found in moist sand and flat seeps, July–Sept., B.

Bouteloua curtipendula (Michx.) Torr. Perennial herb; tree shade in side canyons, Aug.–Sept., W.

Bouteloua gracilis (H.B.K.) Lag. ex Steudel. Perennial herb; found on sandy flats with pinion trees, June–Sept., W.

Bromus carinatus H. & A. Perennial herb; sandy soil in side canyon, May–June, W.

Bromus tectorum L. Annual herb; found on all sandy flats and near streams, April–Sept., B, W.

Dactylis glomerata L. Perennial herb; sandy soil beside creek, July–Aug., B.

Elymus canadensis L. Perennial herb; moist sand near seep, Aug.–Sept.

Elymus cinereus Scribn. & Merr. Perennial herb; sandy soil beside creek, Aug.–Sept.

Elymus elymoides (Raf.) Swezey. Perennial herb; wet sand of seep, April–May, W.

Elymus smithii (Rybd.) Gould. Perennial herb; sandy areas of lower canyon, April–June.

Elymus trachycaulus (Link) Gould ex Shinners. Perennial herb; sandy soil, May–June.

Eremopyrum triticeum (Gaetrn.) Nevski. Annual herb; dry sandy soil beside creek, July–Aug., B.

Glyceria striata (Lam.) A. S. Hitch. Perennial herb; wet sandy soil by seep, June–July.

Hilaria jamesii (Torr.) Benth. Perennial herb; dry sandy soil, June–July.

Hordeum jubatum L. Perennial herb; wet sandy soil by seep, June–July.

Hordeum pusilium Nutt. Annual herb; dry sandy soil, June–July.

Muhlenbergia andina (Nutt.) A. S. Hitch. Perennial herb; found in sandy soil of dry creek bed, Aug.–Sept., W.

Muhlenbergia pungens Thurben in Gray. Perennial herb; dry sandy soil, Aug.–Sept., W.

Monroa squarrosa (Nutt.) Torr. Annual herb; found on sandy soil, July–Aug., W.

Pragmites australis (Cav.) Trin. ex Steudel. Tall perennial herb; found at Betatakin ruin, June–Sept., W.

Poa pratensis L. Perennial herb, moist soil in shade, June–Sept.

Polypogon semiverticillatus (Forsskal) Hylander. Perennial herb, moist, sandy soil, June–July, B.

Puccinellia nuttalliana (Schultes) A. S. Hitch. Perennial herb, sand by seep, June–July.

Schizachyrium scoparium (Michx.) Nash in Small. Perennial herb, sand by seep, July–Aug.

Secale cereale L. Annual herb, moist sand by seeps, July–Aug., B.

Sphenopholis obtusata (Mitchx.) Scribn. Annual herb, wet sandy soil, July–Aug.

Sporobolus cryptandrus (Torr.) gray. Perennial herb, dry sand, Aug.–Sept., W.

Stipa comata Trin. & Rupr. Perennial herb, sandy soil, May–June, W.

Stipa hymenoides R. & S. Perennial herb, dry sand, May–June, W.

Vulpia octoflora Walter. Annual herb, sandy soil creekside, May–June, W.

Typhaceae

Typha domingensis Pers. Perennial, below Keet Seel ruin and side canyons, June–Sept.

Aceraceae

Acer negundo L. Tree, near streams and seeps, May–Oct., W.

Amaranthaceae

Amaranthus blitoides Wats. Annual herb, sandy soil near streams, July–Sept.

Anacardiaceae

Rhus aromatica var. *trilobata* (Nutt.) Gray. Shrub, upper side canyon, June–Aug., W.

Toxicodendron rydbergii (Small) Greene. Small shrub, upper side canyons, June–Sept., W.

Apiaceae

Aletes sessiliflorus Theobald & Tseng. Perennial herb, sand by streams, June–July, new report.

Cymopterus acaulis (Pursh) Raf. Perennial herb, sand under trees, June–July, W.

Cymopterus beckii Welsh & Goodrich. Perennial herb near seeps, June–July, new report, A, C2.

Cymopterus purpureus Wats. Perennial herb, clay soil near trees, June–July.

Apocynaceae

Apocynum cannabium L. Perennial herb, moist sand by seeps, June–Aug.

Apocynum x medium Greene. Perennial herb, moist sand by stream, June–July.

Asclepiadaceae

Asclepias asperula (Decne.) Woodson. Perennial herb, sand, May–June, W.

Asclepias latifolia (Torr.) Raf. Perennial herb, sunny sand, June–July.

Asclepias speciosa Torr. Perennial herb, beside stream, July–Aug., W.

Asclepias subverticillata (Gray) Vail. Perennial herb, sunny canyon sides, June–Aug.

Asteraceae

Ambrosia acanthicarpa Hook. Annual herb, sandy soil, Aug.–Sept., W.

Antennaria neglecta Greene. Perennial herb, shade, sand, May–June, W.

Antennaria parvifolia Nutt. Perennial herb, shade, June, W.

Artemisia absinthium L. Perennial herb, dry sand, July–Aug.

Artemisia campestris L. Perennial herb, dry sandy soil, shade, July–Aug., W.

Artemisia carruthii Wood ex Carruth. Perennial herb, sandy soil, July–Aug.

Artemisia dracunculus L. Perennial herb, shade, June–Aug., W.

Artemisia frigida Willds. Perennial herb, sandy soil, June–Sept., W.

Artemisia ludoviciana Nutt. Perennial herb, moist sand, July–Aug., W.

Artemisia tridentata var. *tridentata* Nutt. Shrub, common in canyon, June–Aug., W.

Aster frondosus (Nutt)T. & G. Annual herb, moist sand, Aug.–Sept., W.

Aster glaucodes Blake. Perennial herb, creekbed, July–Sept.

Brickellia californica Gray. Perennial subshrub, moist sand, July–Aug., W.

Brickellia microphylla (Nutt.) Gray. Small shrub, sandy soil, Aug.–Oct., W.

Brickellia oblongifolia Nutt. Perennial subshrub, dry clays, May–June.

Chaetopappa ericoides (Torr.) Nesom. Perennial herb, dry sand, June–July, W.

Chrysothamnus depressus Nutt. Low shrub, dry creek bottom, July–Sept.

Chrysothamnus nauseosus (Pallas)Britt. Shrub, common in canyon, July–Sept.

Chrysothamnus viscidiflorus (Hook.)Nutt. Shrub, lower canyon, July–Sept., W.

Cirsium calcareum var. *pulchellum* (Greene)Welsh. Perennial herb, creek bottoms, July–Sept.

Cirsium vulgare (Savi)Ten. Biennial herb, creek bottom, July–Sept.

Conyza canadensis (L.)Cronq. Annual herb, creek bottom, June–Sept.

Erigeron bellidiastrum Nutt. Annual herb, sandy soil, July–Aug.

Erigeron compactus Blake. Perennial herb, dry sand, May–June.

Erigeron eatonii Gray. Perennial herb, sand, shade, May–June, W.

Erigeron flagellaris Gray. Perennial herb, near seep, April–May.

Erigeron lonchophyllus Hook. Perennial herb, moist sand, July–Aug.

Erigeron pumilis Nutt. Perennial herb, sandy soil, June–July.

Erigeron speciosus (Lindl.) D.C. Perennial herb, sandy soil July–Aug.

Erigeron utahensis Gray. Perennial herb, sandy soil, sun, May–June.

Gnaphalium chilense Sprengel. Annual herb, moist sand, July–Aug.

Gutierrezia sarothrae (Prush)Britt. & Rusby. Small shrub, sand, sun, July–Sept., W.

Haplopappus ameriodes (Nutt.)Gray. Perennial herb, dry clays, May–June.

Haplopappus spinulosus (Prush)D.C. Perennial herb, sand, shade, July–Aug.

Helianthus petiolaris Nutt. Annual herbs, sand, sun, July–Aug., W.

Heterotheca villosa (Pursh)Shinn. Perennial herb, sandy soil, common, July–Sept., W.

Hymenopappus filifolius Hook. Perennial herb, west facing walls, June–July, W.

Hymenoxys acaulis (Pursh)Parker. Perennial herb, sandy soil, May–June, W.

Lactuca serriola L. Biennial herb, sandy soil, Aug.–Sept., B, W.

Lygodesmia grandiflora (Nutt.)T.&G. Perennial herb, clay soil, June–July.

Machaeranthera canescens (Pursh)Gray. Biennial herb, sandy soil, July–Aug., W.

Machaeranthera grindeliodes (Nutt.)Shinn. Perennial herb, dry sand, June–July, W.

Petradoria pumila (Nutt.)Greene. Perennial herb, dry sand, June–July.

Psilostrophe sparsiflora (Gray)W.Nels. Perennial herb, sandy soil, June–Aug., W.

Senecio douglasii DC. Perennial herb, sandy soil below seep, July–Aug.

Senecio multilobatus T.&G. Perennial herb, sandy soil, shade, May–June, W.

Senecio spartioides T.&G. Perennial herb, sandy soil, Aug.–Sept., W.

Solidago canadensis L. Perennial herb, dry creek bottom, July–Sept., W.

Sonchus asper (L.)Hill. Annual herb, moist sand, July–Sept., B.

Stephanomeria exigua Nutt. Annual herb, sandy soil, July–Aug.

Stephanomeria tenuifolia (Torr.)Hall. Perennial herb, sandy soil, July–Aug.

Tagetes patula L. Annual herb, moist sandy soil, July–Aug., B.

Taraxacum officinale Weber ex Wiggers. Perennial herb, moist soil, May–Sept., B.

Thelesperma subnudum Gray. Perennial herb, sandy soil, sun, June–July, W.

Tragopogon dubius Scop. Biennial herb, dry sand, June–Aug., B.

Verbesina encelioides (Cav.)Benth.&Hook. Annual herb, sandy soil, July–Aug.

Wyethia scabra Hook. Perennial herb, creekbed sand, June–July.

Xanthium strumarium L. Annual herb, moist sand, June–Aug., B.

Berberidaceae

Mahonia repens (Lindl.)G.Don. Small evergreen shrub, shade, W.

Betulaceae

Betula occidentalis Hook. Small trees, along creek sides, May–Aug.

Boraginaceae

Cryptantha bakeri (Greene)Payson. Biennial herb, sandy soil, May–June.

Cryptantha crassisepala (T.&G.)Greene. Annual herb, sand, sun, May–June, W.

Cryptantha flava (A.Nels.)Payson. Perennial herb, sandy soil, May–June.

Cryptantha fulvocanescens (Wats.)Payson. Perennial herb, dry sand, June–July.

Cryptantha inaequata Johnston. Perennial herb, moist sand below seep, June–July.

Cryptantha cinerea (Torr.)Cronq. Perennial herb, sandy soil, sun, May–June.

Cryptantha circumscissa (H.&A.)Johnston. Annual herb, sandy soil, May–June.

Lappula occidentalis (Wats.)Greene. Annual herb, dry sand, April–May, W.

Lithospermum insicum Lehm. Perennial herb, moist sand, June–Aug.

Brassicaceae

Arabis perennans Wats. Perennial herb, sand, shade, June–Aug., W.

Arabis pulchra var. *pallens* Jones. Perennial herb, sandy soil, May–June.

Capsella bursa-pastoris (L.)Medicus. Annual herb, near trails, May–June, B.

Chorispora tenella (Pallas)DC. Annual herb, along trails, June–July, B.

Descurainia pinnata (Walter)Britt. Annual herb, sandy soil, May–June, W.

Descurainia sophia (L.) Webb ex Prantl. Annual herb, trail side, May–June, W.

Dithyrea wislizenni Engelm. in Wisliz. Annual herb, sand, May–June, W.

Lepidium montanum var. *spathulatum* (Robins.)C.L.Hitch. Perennial herb, sandy soil, July–Aug., W.

Lepidium virginicum L. Annual herb, moist sand by seep, July–Aug.

Lesquerella intermedia (Wats.)Heller. Perennial herb, sandy soil, April–June, W.

Pysaria newberryi Gray. Perennial herb, sandy soil, June–July.

Sisymbrium altissimum L. Annual herb, sand dunes, July–Sept., B.

Stanleya pinnata (Pursh)Britt. Perennial herb, clays, June–Aug.

Streptanthella longirostris (Wats.)Rydb. Annual herb, sandy soil, shade, May–June.

Strepthanthus cordatus Nutt. ex T.&G. Perennial herb, sand, shade, June–Aug., W.

Thelypodium integrifolium (Nutt.)Britt.&Rose. Biennial herb, sandy soil, June–Aug.

Thlaspi montanum L. Annual herb, moist sand below seep, April–May.

Cactaceae

Coryphantha vivipara (Nutt.)Britt.&Rose. Perennial, sandy soil, shade, June.

Echinocereus triglochidiatus Englem. Perennial, sandy soil, shade, June.

Opuntia erinacea Englem. Perennial, sandy soil, sun, June.

Opuntia fragilis (Nutt.) Haw. Perennial, sandy soil, shade, June, W.

Opuntia phaeacantha var. *discata* (Griffiths)Benson & Walkington. Perennial, below Betatakin ruin, June.

Opuntia polycantha Haw. Perennial, sandy soil, sun, June.

Opuntia whipplei Engelm. Perennial, sandy soil, sun, June.

Sclerocactus whipplei (Engelm.)Britt.&Rose. Perennial, sandy soil, shade, June.

Cannabaceae

Humulus americanus Nutt. Perennial herb, dry creek bottom, June–July, W.

Capparaceae

Cleome serrulata Pursh. Annual herb, sandy soil, sun, May–July, W.

Caprifoliaceae

Symphoricarpos oreophilius Gray. Shrub, sandy soil, shade, June–Aug., W.

Caryophyllaceae

Arenaria fendleri Gray. Perennial herb, sandy soil, sun, May–June, W.

Silene menziesii Hook. Perennial herb, sandy soil, shade, May–June, W.

Chenopodiaceae

Atriplex canescens (Pursh)Nutt. Shrub, sandy soil, sun, July–Aug.

Atriplex confertifolia (Torr.&Frem)Wats. Shrub, sandy soil, July–Aug.

Atriplex powellii Wats. Annual herb, sandy soil below seep, July–Aug.

Chenopodium album L. Annual herb, sandy soil, shade, June–Aug., B.

Chenopodium leptophyllum (Moq.)Wats. Annual herb, sandy soil, July–Aug.

Chenopodium rubrum L. Annual herb, sandy soil, July–Aug.

Corispermum villosum Rybd. Annual herb, sandy soil, July–Sept.

Kochia scoparia (L.)Schrader. Annual herb, sandy soil, July–Aug., B.

Salsola iberica Sennen & Pau. Annual herbs, sandy soil, sun, July–Sept., B, W.

Sarcobatus vermiculatus (Hook.)Torr in Emory. Shrub, sandy soil, July–Sept.

Suaeda torreyana Wats. Perennial subshrub, sandy soil, July–Aug.

Cornaceae

Cornus sericea L. Shrub, streamside, shade, May–Sept., W.

Elaegnaceae

Elaeagnus angustifolia L. Small tree, near creeks, May–Sept., B.

Shepherdia rotundifolia Parry. Evergreen shrub, cliffsides, W.

Ericaceae

Arctostaphylos patula Greene. Shrub, sand, near creek, May–Sept., W.

Euphorbiaceae

Euphorbia lurida Engelm. Perennial herb, sand, sun, June–Aug.

Euphorbia micromera Boiss. Annual herb, sand, sun, July–Sept.

Fabaceae

Astragalus amphioxys Gray. Perennial herb, dry sand, sun, June–July, W.

Astragalus ceramicus Sheldon. Perennial herb, sandy soil, June–July.

Astragalus cottamii Welsh. Perennial herb, sandy soil, shade, June–July, A, C3.

Astragalus flavus Nutt. ex T.&G. Perennial herb, sandy soil, May–June.

Astragalus lentiginosus Dougl. ex Hook. Perennial herb, sandy soil, sun, May–June.

Astragalus mollissimus Torr. Perennial herb, sandy soil, June–July, W.

Astragalus sesquiflorus Wats. Perennial herb, sand on canyon sides, June–Sept., A, W.

Astragalus zionis Jones. Perennial herb, along trail, May–June, A.

Glycyrrhiza lepidota Pursh. Perennial herb, moist sand, shade, July–Aug.

Lathyrus brachycalyx Rybd. Perennial herb, sand, shade, July–Aug., W.

Lupinus argenteus Pursh. Perennial herb, sand, sun, June–Aug.

Medicago lupulina L. Annual herb, sand near creek, June–July, B.

Medicago sativa L. Annual herb, sandy soil, sun, July–Sept., B.

Melilotus alba Medic. Annual herb, sand, shade, June–July, B.

Psoralidium lanceolatum (Pursh)Rydb. Perennial herb, sandy soil, June–July.

Trifolium repens L. Perennial herb, sand near creek, June–July, B.

Fagaceae

Quercus gambelii Nutt. Small trees, sandy soil, canyon sides, May–Sept., W.

Fumariaceae

Corydalis aurea Willd. Annual herb, sandy soil, shade, June–July, W.

Gentianaceae

Swertia radiata (Kellogg) Kuntze. Perennial herb, sandy soil; June–Sept.

Geraniaceae

Erodium cicutarium (L.)L'Her. Annual herb, sand, sun, May–Sept., W.

Geranium caespitosum James. Perennial herb, sandy soil, shade, June–Aug., W.

Grossulariaceae

Ribes cereum Dougl. Shrub, sand, shade, May–Sept., W.

Ribes inerme Rydb. Shrub, side canyons, shade, June–Sept.

Ribes leptanthus Gray. Shrub, side canyons, shade, June–July, W.

Hydrangeaceae

Fendlera rupicola Gray. Shrub, sandy soil, sun, May–July, W.

Hydrophyllaceae

Nama retrosum J.T. Howell. Annual herb, sand dunes, sun, June–July, A, C3, W.

Phacelia ivesiana Torr. in Ives. Annual herb, sandy soil, sun, May–June.

Lamiaceae

Dracocephalum thymiflorum L. Annual herb, sandy soil, near creek, June–July, B.

Hedeoma drummondii Benth. Annual or perennial herb, sand, June–July.

Marrubium vulgare L. Perennial herb, sandy soil, Aug.–Sept., B.

Mentha arvensis L. Perennial herb, moist sand, shade, Aug.–Sept., W.

Poliomintha incana (Torr.)Gray. Shrub, sandy soil, May–June, W.

Linaceae

Linum aristatum Engelm. Annual herb, sandy soil, Aug.–Sept.

Linum perenne L. Perennial herb, sandy soil, shade, July–Aug.

Loasaceae

Mentzelia albicaulis Dougl. ex Hook. Annual herb, sandy soil, June–July.

Malvaceae

Sphaeralcea parvifolia A. Nels. Perennial herb, sand, sun, May–July.

Nytaginaceae

Mirabilis linearis (Pursh)Heimerl. Perennial herb, sandy soil, July–Aug., W.

Mirabilis multiflora (Torr.)Gray in Torr. Perennial herb, sand, shade, July–Aug.

Mirabilis oxybaphoides (Gray)Gray in Torr. Perennial herb, sandy soil, Aug.–Sept.

Tripterocalyx carneus (Greene)Galloway. Annual herb, sand, sun, July–Aug., W.

Onagraceae

Epilobium ciliatum Raf. Perennial herb, moist sand, shade, June–Aug., W.

Gayophytum racemosum T.&G. Annual herb, dry sand, sun, May–June.

Oenothera caespitosa Nutt. Perennial herb, sand, beside trail, June–July.

Oenothera elata H.B.K. Biennial herb, sandy, shade, July–Sept.

Oenothera pallida Lindl. Annual herb, sand, sun, June–July, W.

Orobanchaceae

Orobanche multiflora Nutt. Perennial herb, near *A. tridentata* Nutt., June–July, W.

Plantaginaceae

Plantago lanceolata L. Perennial herb, sandy soil, beside trails, May–June, B.

Plantago major L. Perennial herb, moist sand, June–Aug., B.

Plantago patagonica Jacq. Annual herb, dry sand, near trail, May–June, W.

Polemoniaceae

Gilia aggregata (Pursh)Sprengel. Perennial herb, sandy soil, sun, June–Aug., W.

Gilia leptomeria Gray. Annual herb, sandy soil, sun, June–July.

Gilia longiflora (Torr.)D.Don. Annual herb, sandy soil, shade, June–July, W.

Leptodactylon pugens (Torr.)Nutt. Subshrub, sand, sun, May–July, W.

Polygonaceae

Erigonum alatum Torr. in Sitg. Perennial herb, sandy soil, sun, May–July, W.

Erigonum cernuum Nutt. Annual herb, sandy soil, Aug.–Sept.

Erigonum microthecum Nutt. Small shrub, sandy soil, Aug.–Sept., W.

Polygonum aviculare L. Annual herb, sandy soil, Aug.–Sept.

Polygonum douglassi Greene. Annual herb, sandy soil, June–July.

Portulaceae

Portulaca oleraceae L. Annual herb, moist sand, June–July.

Portulaca retusa Engelm. Annual herb, sand behind trail, June–July.

Talium parviflorum Nutt. Perennial herb, sandy depressions, May–June.

Primulaceae

Androsace septentrionalis L. Annual herb, sandy soil, shade, June–July, W.

Ranunculaceae

Aquilegia micrantha Eastw. Perennial herb, hanging gardens, June–July, W.

Clematis lingusticifolia Nutt. Woody vine, canyon sides, shade, June–July, W.

Delphinium andersonii Gray. Perennial herb, sand along trail, June–July, W.

Ranunculus cymbalaria Pursh. Perennial herb in marshy areas, May–Sept., W.

Ranunculus testiculatus Crantz. Annual herb, sandy soil, sun, May–June, B.

Thalictrum fendleri Engelm. Perennial herbs, sand, shade, June–Aug., W.

Rhamnaceae

Rhamnus betulifolia Greene. Shrub, above pool, shade, June.

Rosaceae

Amelanchier alnifolia (Nutt.)Nutt. Shrub, sandy soil, shade, May–June.

Amelanchier utahensis Koehne. Shrub, sandy soil, sun, May–June, W.

Cercocarpus intricatus Wats. Shrub, sand, sun, May–June, W.

Cercocarpus montanus Raf. Shrub, sandy soil, partial shade, June–July.

Holodiscus dumosus (Nutt.)Heller. Shrub, sandy soil, June–July, W.

Prunus angustifolia Marsh. Small trees, Keet Seel ruin, May–July.

Prunus virginiana L. Small tree, beside streams, June–July, W.

Pursia mexicana (D.Don)Welsh. Shrub, sandy soil, sun, May–June, W.

Pursia tridentata (Pursh)DC. Shrub, sandy soil, sun, May–June, W.

Rubiaceae

Galium aparine L. Annual herb, moist sand, shade, June–Aug.

Salicaceae

Populus angustifolia James. Tree, sandy soil, by streams, May.

Populus fremontii Wats. Tree, sand, along streams, May.

Salix exigua Nutt. Shrub, sand, sun, along streams, May–June.

Salix laevigata Bebb. Small tree, sand, along stream, May–June, W.

Salix lasiolepis Benth. Shrub, sand, along stream, May–June.

Salix monticola Bebb. ex Coult. Shrub, moist sand, May–June.

Santalaceae

Comandra umbellata (L.)Nuatt. Perennial herb, sandy soil, sun, June–July, W.

Saxifragaceae

Heuchera parvifolia Nutt. in T.&G. Perennial herb, sandy soil, shade, June–July, W.

Scrophulariaceae

Castilleja chromosa A. Nels. Perennial herb, sandy soil, June–July.

Castilleja linariifolia Benth. Perennial herb, sandy soil, shade, May–June, W.

Cordylanthus wrightii Gray. Annual herb, sandy soil, shade, July–Aug., W.

Mimulus eastwoodiae Rydb. Perennial herb, hanging gardens, July–Aug.

Mimulus guttatus DC. Perennial herb, moist sand, shade, June–July.

Mimulus rubellus Gray. Annual herb, sandy soil, shade, July–Aug.

Penstemon barbatus (Cav.)Roth. Perennial herb, sand, July–Aug., W.

Penstemon comarrhenus Gray. Perennial herb, sand, sun, June–July, W.

Penstemon eatonii var. *undosus* Jones. Perennial herb, sand, shade, May–June, W.

Penstemon pseudoputus (Crosswhite) N.Holmgren. Perennial, sand, June–July, A, C3.

Penstemon rostriflorus Kellogg. Perennial, sand, shade, June–July.

Verbascum thapsus L. Biennial, sand, sun, July–Aug., B.

Veronica pergrina L. Annual herb, moist sand, June–July.

Solanaceae

Chamaesaracha coronopus (Dunal)Gray. Perennial herb, sandy soil, Aug.–Sept., W.

Datura wrightii Regel. Annual herb, sandy soil, partial shade, July–Aug.

Lycium pallidum Miers. Shrub, sand, sun, May–June, W.

Pysalis hederifolia Gray. Perennial herb, sand, sun, July–Aug.

Solanum jamesii Torr. Perennial herb, sand, by trail, July–Aug., W.

Tamaricaceae

Tamarix ramosissima Ledeb. Shrub, sand, along washes, May–June, B.

Ulmaceae

Ulmus pumila L. Tree, along sides of creek, May–June, B.

Valerianaceae

Valeriana acutiloba Rybd. Annual herb, sand, shade, July–Aug., W.

Verbenaceae

Verbena bracteata Lag.&Rodr. Perennial herb, sand, sun, Aug.–Sept.

Viscaceae

Phorodendron juniperinum Gray. Parasitic perennial, found on juniper trees.

Zygophyllaceae

Tribulus terrestris L. Annual herb, sand, sun, July–Aug., B.

MIXED CONIFER AND RED FIR FOREST STRUCTURE AND USES IN 1899 FROM THE CENTRAL AND NORTHERN SIERRA NEVADA, CALIFORNIA

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ABSTRACT

Historical data collected from five "average" mixed conifer stands, four large mixed conifer stands, and four red fir stands from the central and northern Sierra Nevada by George Sudworth in 1899 were analyzed to determine historic forest structure including diameter distributions, basal areas, and snag and live tree densities. The effects of early logging operations on stand composition and structure is quantified by comparing characteristics of the trees that were harvested versus those unharvested in four mixed conifer stands. Average diameter at breast height (DBH) was 86 cm (34 inches) in the "average" mixed conifer stands, 110 cm (43 inches) in the large mixed conifer stands (this was equal to the average DBH of 8 mixed conifer stands sampled by Sudworth in the southern Sierra Nevada), and 77 cm (30 inches) in the red fir stands for trees greater than 30.5 cm DBH. Shade intolerant tree species dominated the "average" mixed conifer stands, shade intolerant, intermediate, and shade tolerant species were abundant in the large mixed conifer stands, and *Abies magnifica* Andr. Murray dominated the red fir stands. Mean tree density for the "average" mixed conifer, large mixed conifer, and red fir stands was 229 trees/ha, 235 trees/ha, and 433 trees/ha, respectively. Average tree density was higher in Sudworths southern Sierra Nevada mixed conifer stands when compared to the central and northern Sierra Nevada. Snag density averaged 5/ha in the large mixed conifer stands and 17.5/ha in the red fir stands. Early logging operations removed the majority of the *Pinus* spp. and *Pseudotsuga menziesii* (Mirbel) France leaving large amounts of *Calocedrus decurrens* (Torrey) Florin and *Abies concolor* (Gordon & Glend.) Lindley. Information from this study can assist in the characterization of historic stand structure in these forest types.

The absence of fire in the 20th century and past harvesting operations have modified the structure and ecosystem processes in the coniferous forests of the Sierra Nevada. An increase in the density of small shade tolerant trees has been produced in many forest types (Leopold et al. 1963; Hartesveldt and Harvey 1967; Vankat and Major 1978; Parsons and DeBendeetti 1979; Bonnicksen and Stone 1982) and this increase has resulted in a decrease in forest sustainability (Weatherspoon and Skinner 1996; van Wagtendonk 1996; Stephens 1998). Changes in climate over the last centaury may have also contributed to the changes in forest structure (Millar and Woolfenden 1999).

Historical and prehistoric information on the structure (density, size distribution, and species composition) of mixed conifer forests are relatively rare and they have been reviewed elsewhere (Stephens and Elliott-Fisk 1998). One of the methods that can be used to determine prehistoric forest structure is the analysis of data from early forest inventories. These data provide quantitative information on historic forest structure, however, the results from the analyses can be biased because the methods used to select the stands were frequently not recorded (Stephens and Elliott-Fisk 1998).

Analysis of historical data have been done for the Stanislaus and Lake Tahoe Forest Reserves (Sudworth 1900), portions of the northern Sierra Nevada and the Transverse Ranges of southern California (McKelvey and Johnston 1992), and portions of the southern Sierra Nevada (Stephens and Elliott-Fisk 1998). All of these studies discuss early logging operations but no work has been done that quantifies the effects of early logging at the stand level, quantifies the amount of hardwoods present historically in mixed conifer forests, determines historic snag densities and sizes, or differentiates between average and mature mixed conifer stands.

Early logging operations affected the composition and structure of Sierra Nevada forests, especially between 1860 and 1950 (Laudenslayer and Darr 1990). In 1899, approximately 45 percent of the trees harvested in California were either *Pinus ponderosa* Laws (ponderosa pine) or *Pinus lambertiana* Douglas (sugar pine). Most early logging operations in the Sierra Nevada harvested all trees that were considered to be merchantable at the time of the harvest (Laudenslayer and Darr 1990).

The viability of the California spotted owl (*Strix occidentalis occidentalis*) is receiving major atten-

tion in California. The owl prefers to nest in mixed conifer forests with 80 percent of the nesting sites occurring in this forest type followed by 10 percent in *Abies magnifica* Andr. Murray (red fir) and 7 percent in *Pinus ponderosa* hardwood forests (Verner et al. 1992). The remaining 3 percent of nests occur in eastside pine forests and foothill riparian-hardwood habitats in the western Sierra Nevada foothills (Verner et al. 1992).

The habitat requirements of the California spotted owl have been investigated and it nests in old-growth forests with high canopy cover (Gutierrez et al. 1992). A relatively high number of snags and down logs are also correlated to the current nesting sites of the California spotted owl (Gutierrez et al. 1992) but no prehistorical data exist on the abundance of snags or fuel loads in this forest type making it difficult to describe the composition of the prehistorical habitat.

The objective of this paper is to analyze mixed conifer and red fir forest inventory data acquired by George Sudworth in 1899 from the central and northern Sierra Nevada to further our understanding of forest conditions and their management in the late 19th century. Analysis includes snag and live tree densities, basal areas, diameter distributions, and quantification of the effects of early logging operations on stand composition and structure.

STUDY SITE AND METHODS

The historic data analyzed in this paper were obtained from the area of the central and northern Sierra Nevada that now includes the southern portion of the Tahoe National Forest, the El Dorado National Forest, and northern portion of the Stanislaus National Forest.

Mixed conifer and red fir forests were surveyed in 1899 by George B. Sudworth while employed by the United States Geological Survey. The purpose of this survey was to inventory the forest reserves of the Sierra Nevada. The original unpublished field notebooks (Sudworth 1899) were the source of the inventory data analyzed in this paper.

Sierra Nevada mixed conifer forests sampled by Sudworth were composed of white fir *Abies concolor* (Gordon & Glend.) Lindley (white fir), *Abies magnifica, Pinus ponderosa, Pinis lambertiana, Pinis jeffreyi* Grev. and Balf (Jeffrey pine), *Calocedrus decurrens* (Torrey) Florin (incense cedar), *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir), and *Quercus kelloggii* Newb. (California black oak). The red fir forests were composed of *Abies magnifica, Pinus jeffreyi, Pinus monticola* Douglas (western white pine), *Pinus contorta* spp. *murrayana* (Grev. & Balf.) Critchf. (lodgepole pine), and *Tsuga mertensiana* (Bong.) Carrière (mountain hemlock). Red fir forests are widely distributed and they can be found on both the west and east sides of the Sierra Nevada (Rundel et al. 1977).

All stand data recorded by Sudworth in 1899 are analyzed in this paper with the exception of one stand located in a pure *Pinus jeffreyi* forest because of no replication in this forest type. Exact stand locations are not given in the field notebooks but references to rivers, mountains, and landmarks are included (Sudworth 1899).

Five "average" mixed conifer stands, four large mixed conifer stands, and four red fir stands were recorded in the 1899 field notebooks (Sudworth 1899). Mixed conifer stand data were stratified into two classes (average and large) whereas this was not done in the southern Sierra Nevada analysis (Stephens and Elliott-Fisk 1998) because no stands were identified by Sudworth in his notebooks as having "average" characteristics.

Sudworth recorded the species, diameter at breast height (DBH), and number of 4.9 m (16 ft) logs for each tree greater than 30.5 cm (12 inches) DBH (one 28 cm DBH tree was recorded in a red fir stand). Each stand was sampled with one 0.1 ha (0.25 acres) plot. He recorded notes on regeneration (estimate of density by species, not a complete seedling inventory), forest floor depth, and other information such as the revenue generated by early logging operations. He also frequently commented on the effects of early grazing and burning on the Sierra Nevada and his comments are summarized below.

The following values were calculated by averaging all stand data for each of the 3 forest types ("average" mixed conifer, large mixed conifer, red fir): number of snags per hectare, snag basal area, diameter and species of trees removed by early logging operations, basal area per hectare by species, number of trees per hectare by species (density), quadratic mean diameter by species, percent total basal area by species, and percent total stocking by species.

Stand data are summarized and discussed, but a statistical analysis was not performed. Selection of an appropriate analysis method requires information on sampling procedures which are unknown for this early forest inventory (Stephens and Elliott-Fisk 1998).

RESULTS

"Average" mixed conifer stands. The five mixed conifer stands denoted as "average" by George Sudworth were dominated by moderate sized trees of several species. The average quadratic mean diameter for all trees over 30.5 cm DBH was 86 cm (34 inches). Average tree density was 229 trees/ha (92 trees/acre) (range 150–300 trees/ha). Average basal area was 130 m²/ha (558 ft²/acre) (range 94–186 m²/ha). Table 1 summarizes all stand calculations for the "average" mixed conifer stands.

The largest trees in the "average" mixed conifer stands were *Pinus lambertiana* with an average DBH of 108 cm (42 inches). The largest *Pinus lambertiana* recorded in the inventory had a DBH of

TABLE 1. AVERAGE CALCULATIONS OF GEORGE SUDWORTH'S 5 "AVERAGE" MIXED CONIFER STANDS IN THE CENTRAL AND NORTHERN SIERRA NEVADA IN 1899 (STANDARD ERROR). * Average value for all stands.

Tree	Basal area (m²/ha) [130]*	Trees/ha [229]*	DBH (cm) [86]*	Percent of total basal area	Percent of trees/ha
Abies concolor	5.3 (5.2)	6.0 (6.0)	105.7 (0)	4	3
Calocedrus decurrens	26.0 (6.6)	54.0 (11.2)	80.6 (10.5)	20	24
Pinus lambertiana	8.8 (4.2)	12 (7.4)	107.8 (22.8)	7	5
Pinus ponderosa	56.6 (23.1)	106.0 (37.0)	83.9 (12.1)	43	46
Pseudotsuga menziesii	30.9 (20.2)	38.0 (24.6)	101.2 (1.8)	24	16
Quercus kelloggii	2.4 (1.4)	13.3 (3.7)	58.0 (7.2)	2	6

152 cm (60 inches). *Pinus ponderosa* was the most common species comprising 46 percent of total stocking and 44 percent of total basal area (Table 1).

Abies concolor was rare in the stands accounting for only 3 percent of total stocking and 4 percent of total basal area. *Calocedrus decurrens* and *Pseudotsuga menziesii* were the next most common species, after *Pinus ponderosa,* respectively. The average DBH of the *Quercus kelloggii* was the smallest of the species found in the mixed conifer stands, the conifer with the smallest average DBH was *Calocedrus decurrens* (Table 1).

Pinus lambertiana, Pseudotsuga menziesii, and *Abies concolor* all had similar average DBH's of approximately 105 cm whereas *Pinus ponderosa* and *Calocedrus decurrens* had average DBH's of approximately 82 cm. *Quercus kelloggii* accounted for an average of 6 percent of stand stocking. No snags were recorded in the average mixed conifer stands (Table 2).

Four of the "average" mixed conifer stands inventoried by Sudworth were in the process of being harvested in 1899. Sudworth's notebooks recorded the diameter and species of all trees harvested and also recorded the same information on all trees that remained after the harvesting operation.

All of the *Pseudotsuga menziesii* trees in these

four stands were harvested along with 88 percent of the *Pinus lambertiana* trees (Table 3). The majority of the wood harvested from these stands was from *Pinus ponderosa* trees with an average of 64 m²/ha (275 ft²/acre) removed and this was 2.4 times greater than *Pseudotsuga menziesii* which was the next most common species harvested. The amount of *Calocedrus decurrens* and *Abies concolor* trees harvested was low, averaging 13 percent and 33 percent, respectively (Table 3).

The following comments were written by George Sudworth in the original field notebooks and include information about regeneration and impacts from early European settlers (Sudworth 1899).

September 27, 1899. Near Beech Sawmill (above Placerville) on Big Iowa Canyon. No reproduction (manzanita brush) but abundant a few yards distant. Grazed, no humus, all trees fire marked.

September 28, 1899. South of Blair Sawmill (near Sly Park) on summit of ridge. All touched with fire, humus 1–2 inches in spots. Ample reproduction of all species in patches.

September 30, 1899. Sample on big hill south west of Grizzly Flat 0.5 mile. Humus all burned off.

October 5, 1899. 2 miles east of Whitmore's Mill

TABLE 2. CHARACTERISTICS OF SNAGS FOUND IN MIXED CONIFER AND RED FIR STANDS IN THE CENTRAL AND NORTHERN SIERRA NEVADA IN 1899.

Stand type	Average density (snags/ha)	Density range (snags/ha)	Average DBH (cm)	Average basal area (m²/ha)
Average mixed conifer	0	0	0	0
Large mixed conifer	5	0–10	108.7	4.6
Red fir	17.5	0–60	57.3	4.5

TABLE 3. AVERAGE AMOUNT HARVESTED IN 4 "AVERAGE" MIXED CONIFER STANDS LOCATED IN THE CENTRAL AND NORTHERN SIERRA NEVADA IN 1899.

Tree	Trees/ha cut (percent)	Basal area cut (percent)	Basal area cut (m²/ha)	DBH of trees cut (cm)
Abies concolor	33.3	48.2	3.9	127
Calocedrus decurrens	12.5	12.5	1.6	88.9
Pinus lambertiana	87.5	92.8	17.1	104.3
Pinus ponderosa	57.9	64.2	64.3	103.3
Pseudotsuga menziesii	100.0	100.0	27.2	101.7
Quercus kelloggii	25.0	38.1	2.9	86.4

Fig. 1. El Dorado county, 1899. Opposite Snyder and Sherman's Ranch. Yellow pine (mixed conifer) forest on south slope of Silver Fork. Ponderosa pine 91–193 cm (36–76 inches) in diameter, 46–50 m high (150–165 feet), clear 8–11 m (25–35 feet), ten in 0.1 ha (0.25 acre), 3–5 white fir (*Abies concolor*) same size. Cattle grazed.

(Mill Creek, near Volcano), representing no cut stumpage, rolling flat 1000 feet above creek bottom. No humus, frequent burning destroyed all. Abundant reproduction of pines and cedar 5–8 years old, mostly under 4.

October 5, 1899. Near Whitmore's Mill but in shallow ravine. Taken as a whole mill operator estimates output 10–20 thousand per acre. Abundant reproduction of all species. *Taxus brevifolia* Nutt., dogwood, and *Acer macrophyllum* Pursh abundant. Humus in part 3–6 inches.

Large mixed conifer stands. The four large mixed conifer stands were dominated by large trees of several species and the average quadratic mean diameter at breast height was 110 cm (43 inches) for all trees above 30.5 cm DBH. Average tree density was 235 trees/ha (94 trees/acre) (range 160–300 trees/ha). Average basal area was large 215 m²/ha (923 ft²/acre) (range 188–232 m²/ha). The stands inventoried by Sudworth were relatively open and dominated by large trees (Fig. 1). Table 4 summarizes all stand calculations for the large mixed conifer stands.

Abies concolor was the most common species comprising 46 percent of total stocking, but only accounting for 34 percent of total basal area because of their relatively small diameters. The largest tree inventoried in these stands was a *Pseudotsuga menziesii* and it had a DBH of 188 cm (74 inches). *Pseudotsuga menziesii* made up only 16 percent of the trees/ha but contributed 24 percent of the basal area of the stands because of their large size. *Abies concolor* trees were much more common in the large mixed conifer stands when compared to the "average" mixed conifer stands (46 percent stocking versus 3 percent stocking, respectively).

Abies concolor, Abies magnifica, and *Calocedrus decurrens* were the smallest trees with average quadratic mean diameters of approximately 93 cm. *Pinus ponderosa* and *Pinus lambertiana* were larger with average diameters of approximately 112 cm,

TABLE 4. AVERAGE CALCULATIONS OF GEORGE SUDWORTH'S 4 LARGE MIXED CONIFER STANDS IN THE CENTRAL AND NORTHERN SIERRA NEVADA IN 1899 (STANDARD ERROR). * Average value for all stands.

Tree	Basal area (m²/ha) [215]*	Trees/ha [235]*	DBH (cm) [110]*	Percent of total basal area	Percent of trees/ha
Abies concolor	72.3 (20.0)	107.5 (38.2)	97.3 (6.4)	34	46
Calocedrus decurrens	26.7 (9.5)	32.5 (6.3)	92.0 (17.4)	12	14
Pinus lambertiana	33.4 (18.3)	27.5 (4.8)	109.1 (20.5)	16	12
Pinus ponderosa	10.5 (10.5)	10.0 (10.0)	115.3 (0)	5	4
Pinus jeffreyi	13.8 (11.4)	10.0 (7.1)	120.4 (21.4)	6	4
Pseudotsuga menziesii	51.8 (45.4)	37.5 (31.2)	123.7 (11.8)	24	16
Abies magnifica	6.2 (6.2)	10.0 (10.0)	88.9 (0)	3	4

and the largest trees were *Pinus jeffreyi* and *Pseudotsuga menziesii* with average diameters of approximately 122 cm. *Quercus kelloggii* was not recorded in any of the large mixed conifer stands.

Snag density averaged 5/ha with a range 0–10/ha (Table 2). Average snag quadratic mean diameter was 109 cm and snag average snag basal area was 4.6 m²/ha.

The following comments were written by George Sudworth in the original field notebooks and include information about regeneration and impacts from early European settlers (Sudworth 1899).

September 3, 1899. 12–15 miles west of Bloods, north slope of Mokelumne River. 30 concolor 2–8 inches diameter, 100 under 6 inches. 5 sugar pine under 2 feet high. Thickets of *Acer oblusifobium (glabrum?)*.

September 8, 1899. South slope of Bear River, one half way up slope. Seedlings of all in spots near blue ceonothus when protected from tramping of cattle. No sheep here, but no humus. Abundant blue ceonothus chaparral.

September 9, 1899. South lower slope of Silver Fork (American River) in rich bottom bench (at point where a little stream enters Silver Fork). Dense fir and cedar on outskirts, no seedlings within. Humus 2–3 inches, cattle grazing and sheep.

September 21, 1899. 1.5 miles south of Merzns, across (west) of Dark and Multon Canyons (where Georgetown road crosses). South slope of South Fork of the Consumnes River (?) (Sudworth included the? mark and was probably referring to the American River). Abundant reproduction of all species 1–12 years old, all fire marked 15 years back. Humus 1.5 inches deep, soil sandy loam with rock.

Red fir stands. Sudworth sampled four red fir stands during this inventory and all stands were dominated by *Abies magnifica*. The average quadratic mean diameter at breast height was 77 cm (30 inches) for all trees inventoried. Average tree density was 433 trees/ha (173 trees/acre) (range 180–610 trees/ha) for trees greater that 28 cm DBH. Average basal area was 202 m²/ha (867 ft²/acre) (range 98–286 m²/ha). Table 5 summarizes all stand calculations for the red fir stands.

TABLE 5. AVERAGE CALCULATIONS OF GEORGE SUDWORTH'S 4 RED FIR STANDS IN THE CENTRAL AND NORTHERN SIERRA NEVADA IN 1899 (STANDARD ERROR). * Average value for all stands.

Tree	Basal area (m²/ha) [202]*	Trees/ha [433]*	DBH (cm) [77]*	Percent of total basal area	Percent of trees/ha
Pinus jeffreyi	32.2 (32.2)	25.0 (25.0)	128.1 (15.1)	16	6
Abies magnifica	136.2 (55.3)	272.5 (93.5)	80.1 (10.9)	67	63
Pinus monticola	11.3 (8.0)	30.0 (19.2)	66.4 (19.4)	6	7
Pinus contorta	12.6 (12.6)	70.0 (70.0)	47.8 (12.0)	6	16
Tsuga mertensiana	9.3 (9.3)	35.0 (35.0)	58.0 (14.5)	5	8

Fig. 2.   Amador county, 1899. Near sawmill 5–6 km (3–4 miles) below dam on Bear River. Forest fire in fir and pine, killed all seedlings, just started.

The largest trees in the red fir stands were *Abies magnifica* and *Pinus jeffreyi* with DBH's of 160 cm (63 inches). *Abies magnifica* was the most common tree in the stands accounting for 63 percent of all trees inventoried and 68 percent of average stand basal area (Table 5). The next most common tree found was *Pinus contorta* which accounted for 16 percent of all trees but only contributed to 6 percent of basal area because of the smallest DBH of any species in this forest type.

Snag density averaged 17.5 per ha with a range 0–60 per ha (Table 2). Average snag quadratic mean diameter was 57 cm (22 inches) and average snag basal area was 4.5 m²/ha.

The following comments were written by George Sudworth in the original field notebooks and include information about regeneration and impacts from early European settlers (Sudworth 1899).

September 2, 1899. On foothill (above) Bear Meadow, north fork of Stanislaus River. No grazing, 40 young trees under 10 inches diameter. Humus 4–6 inches deep, no herbaceous growth. 75–100 seedlings 2–10 inches.

September 7, 1899. On south slope 4–5 miles down on Silver Fork (near Silver Lake and Kirkwood). Sheep grazing, no reproduction. Scattered bunches of blue ceonothus. Earth bare, rock and gravel.

September 7, 1899. North side of Thimble Peak (west of Kirkwood Meadow). On volcanic and granite. No humus, grazed by sheep. Dense shade in part, no reproduction. 2 *Abies magnifica* down.

September 13, 1899. On Rocky flat between Lyons and Blakley (south fork Silver Creek, west side of Pyramid Peak). Abundant 1 year fir seedlings, 50 fir under 10 feet, 20 Murr (*Pinus contorta*) pines 2–10 feet, 5 Pimo (*Pinus monticola*) 1–3 feet. Humus 1 inch. Cattle grazed, no sheep within 5 years.

DISCUSSION

Sudworth's noted recent evidence of fire in many stands and believed fires were ignited by sheep herders to increase forage production and by loggers to consume slash fuels (Fig. 2). This burning apparently did not spread extensively because fire scar analysis in the Sierra Nevada have documented the almost complete removal of surface fires in

FIG. 3.   Calvaras county, 1899. About 3 km (2 miles) south west of Bloods. Sandy ridge grazed clean and bare by sheep, gullying.

many mixed conifer forests in the 1860–1870's (Kilgore and Taylor 1979; Swetnam et al. 1990; Swetnam et al. 1992; Caprio and Swetnam 1995) at the same time burning was reportedly being used by loggers and sheep herders (Sudworth 1900; McKelvey and Johnston 1992; Stephens and El-liott-Fisk 1998).

Regeneration was noted in the majority of "average" mixed conifer stands. More site resources (light, water, nutrients) were probably available for regeneration in the "average" mixed conifer stands because of their lower stocking and basal areas. Regeneration in mixed conifer forests probably occurred prehistorically when small gaps were created by the interaction of fire and locally high fuel loads (Stephens et al. 1999).

Regeneration was noted in half of the red fir stands and livestock grazing was noted in all stands. Sudworth noted that in some high elevation sites sheep were actually grazing on conifer seedlings (Sudworth 1899). Many photos in the collection show complete bare mineral soils (Fig. 3) and seedlings were reportedly also trampled by livestock.

Early logging operations had a dramatic effect on the species composition and diameter distributions of mixed conifer stands sampled by Sudworth (Table 3). The majority of the *Pinus* spp. and *Pseudotsuga menziesii* were harvested in the stands leaving large amounts of *Calocedrus decurrens* and *Abies concolor* (Fig. 4). This type of logging operation has been described as "high-grading" because of the preference for large trees of particular genera. In this period it was common for all merchantable trees to be removed during logging operations (Laudenslayer and Darr 1990). *Abies concolor* and *Calocedrus decurrens* were therefore left because they were of relatively low economic value late in the 19th centaury.

Early logging operations coupled with a national fire suppression policy that began in the early 20th century favored shade tolerant species such as *Calocedrus decurrens* and *Abies concolor*. Climate changes over this period (wetter than average) may

Fig. 4. El Dorado county, 1899. Forest logged out 5–6 years ago. Sugar pine (*Pinus lambertiana*), large ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*) taken out, Kellogg oak (*Quercus kelloggii*) and incense cedar (*Calocedrus decurrens*), 12–25 per ha., remain (5–10 per acre). Reproduction of incense-cedar, ponderosa pine, white fir, and Douglas-fir abundant 2–9 m high (6–30 feet), 2–8 years old. Ground grazed. Half mile south of Blairs Mill at Sly Park. Humas 4–10 cm deep (2–4 inches). Soil deep brown, sandy loam.

have also led to an increase in tree densities in Sierra Nevada forests.

The management of *Quercus kelloggii* is receiving increased attention in the Sierra Nevada Framework Project (SNFP) Environmental Impact Statement because several rare species such as the California spotted owl and Pacific fisher use this species for foraging and denning habitat (USDA 2000). *Quercus kelloggii* is shade intolerant, and therefore, would have difficulty living in areas dominated by large mixed conifers because it can be over-topped and killed which is one explanation of why it was not recorded in any large mixed conifer stands. *Quercus kelloggii* did contribute to 6 percent of average stand stocking on the less stocked "average" mixed conifer stands because these stands were composed by smaller trees, and therefore, more site resources were probably available for the oaks.

There was a great deal of variability in snag den-

sities in the stands, particularly in the red fir forest type. Tree density was also much higher in the red fir forest type when compared to the mixed conifer forests. Snag basal area was almost identical in the large mixed conifer stands and red fir stands (4.6 m^2/ha and 4.5 m^2/ha, respectively). Snag densities found in the large mixed conifer stands are on the lower end of the current requirements for California spotted owls (Verner et al. 1992). Very little snag information exists for red fir forests making it difficult to compare this historic data to contemporary data.

The average basal area recorded in the mixed conifer stands is high, even for those labeled as "average." The SNFP Environmental Impact Report is defining desired conditions in mixed conifer forests as having basal areas below 70 m^2/ha (300 ft^2/acre). The large mixed conifer stands Sudworth inventoried had over three times this basal area and the "average" mixed conifer stands had double the

basal area. Some areas of mixed conifer forest in the Sierra Nevada have the ability to produce much larger trees.

The average quadratic mean diameter of the large mixed conifer stands from this study (110 cm) is equal to those recorded in the 8 mixed conifer stands in the southern Sierra Nevada (110 cm) for all trees greater than 30.5 cm DBH. (Stephens and Elliott-Fisk 1998). Omitting *Sequoiadendron giganteum* (Lindley) Buchholz (giant sequoia) data from the four *Sequoiadendron giganteum* –mixed conifer stands in the southern Sierra Nevada produced an average DBH of the remaining trees of 111 cm which is also very similar to those recorded above.

Average tree density was higher in the southern Sierra Nevada when compared to the central and northern Sierra (278 trees/ha compared to 235 trees/ha, respectively). Average stand basal area was also higher in the mixed conifer stands from the southern Sierra Nevada when compared to the large mixed conifer stands from this study (271 m²/ha versus 215 m²/ha, respectively). Since the average DBH was equal in the mixed conifer stands the increase in basal area is a result of increased stocking in the southern Sierra Nevada (18 percent higher).

Abies concolor was very rare in the "average" mixed conifer stands but was the most common tree in the large mixed conifer stands. Low amounts of *Abies concolor* in the "average" mixed conifer stands may have occurred because these stands were probably less developed (younger) or they may have been in drier locations which would have favored pines over true fir species. In the southern Sierra Nevada *Abies concolor* contributed to 40 percent of average stand stocking and 28 percent of average stand basal area (Stephens and Elliott-Fisk 1998). In the large mixed conifer stands in this study, *Abies concolor* contributed to 46 percent of average stand stocking and 34 percent of average stand basal area indicating that *Abies concolor* was slightly more common in the central and northern Sierra Nevada stands sampled by George Sudworth.

Pinus lambertiana was much more common in the southern Sierra Nevada when compared to the central and northern Sierra Nevada (19 percent of stocking, 36 percent of basal area versus 12 percent of stocking, 16 percent of basal area, respectively). This difference can be partially explained by the presence of *Pseudotsuga menziesii* in relatively large amounts (16 percent of stocking, 24 percent of basal area) in the northern Sierra Nevada whereas *Pseudotsuga menziesii* is not native to the southern Sierra Nevada. Both *Pseudotsuga menziesii* and *Pinus lambertiana* are classified as shade intermediate (in between shade tolerant and shade intolerant) and therefore, *Pseudotsuga menziesii* may have occupied areas that *Pinus lambertiana* could have also dominated.

Conclusion

The mixed conifer stands sampled by George Sudworth in 1899 were dominated by large trees at relatively low densities. Shade intolerant species, particularly *Pinus ponderosa,* dominated the "average" mixed conifer stands whereas the large mixed conifer stands were composed of shade tolerant, intermediate, and shade intolerant species.

Early harvesting operations removed the majority of the economically viable species (*Pinus* spp. and *Pseudotsuga menziesii*) and left a large amount of *Calocedrus decurrens* and *Abies concolor.* This practice coupled with fire suppression policies initiated at the beginning of the 20th century promoted the establishment and growth of shade tolerant species.

There was a large amount of variability in snag densities, particularly in the red fir stands. The red fir stands had the highest tree densities and *Abies magnifica* dominated in these stands.

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OLD-GROWTH FOREST ASSOCIATIONS IN THE NORTHERN RANGE OF COASTAL REDWOOD

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ABSTRACT

Old-growth *Sequoia sempervirens* (D. Don) Endl. (redwood) forests occurring in northwestern California and southwestern Oregon were classified and described using data from 206 systematically placed plots. Data were collected from Jedediah Smith Redwoods State Park, Del Norte Coast Redwoods State Park, northern Redwood National Park, and the southwestern portion of the Siskiyou National Forest. Plot data were analyzed using TWINSPAN and polar ordination. Six associations within the redwood series were classified: *Sequoia sempervirens/Polystichum munitum* (Kaulf) C. Presl (SESE/POMU), *Sequoia sempervirens-Pseudotsuga menziesii* (Mirbel) Franco/*Rhododendron macrophyllum* D. Don (SESE-PSME/RHMA), *Sequoia sempervirens-Tsuga heterophylla* (Raf.) Sarg./*Vaccinium ovatum* Pursh (SESE-TSHE/VAOV), *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* (SESE-TSHE/POMU), *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* Pursh (SESE-TSHE/RUSP), and *Sequoia sempervirens-Alnus rubra* Bong./*Rubus spectabilis* (SESE-ALRU/RUSP).

Discriminant analysis was used to assess the relationships between abiotic site variables and classified floristic associations. Elevation and coastal proximity explained 81.1 percent of the variation among associations. Aspect and topographic position explained 14.2 percent of the remaining variation. Moisture was the primary environmental variable controlling the distribution of classified forest associations.

Sequoia sempervirens (D. Don) Endl. (redwood) forests are endemic to coastal margins and mesic inland sites from central California to southern Oregon. Along this broad latitudinal gradient, *S. sempervirens* is limited to a narrow belt 10 to 50 kilometers wide (Roy 1966; Fox 1989). The extreme northern range of *S. sempervirens* has not been adequately classified and described. Vast tracts of old-growth forest in Jedediah Smith Redwoods State Park, Del Norte Coast Redwoods State Park, and northern sections of Redwood National Park have been virtually ignored in the *S. sempervirens* literature. The difficult access, steep terrain, and huge volume of coarse woody debris characterizing interior portions of these parks may explain the dearth of botanical information in the region. As a result of this relative isolation, these parks contain some of the most primeval and undisturbed old-growth (Helms 1998) redwood vegetation in existence. Southwestern Siskiyou National Forest contains a patchy network of old-growth representing the northernmost natural *S. sempervirens* stands. Since they exist at the terminus of the redwood range, these stands are ecologically significant. They may give insight into processes affecting other parts of the range, including gradients in soil moisture and temperature that affect species composition and stand dynamics.

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METHODS

Study Area. The northern range of redwood, as defined in this study, includes Jedediah Smith Redwoods State Park, Del Norte Coast Redwoods State Park, and northern Redwood National Park, all located in northern California, and portions of Siskiyou National Forest located in southwestern Oregon. It extends from 41°47′N to 42°10′N, and 124°4′W to 124°12′W. The study area is topographically diverse—elevations range from sea level to over 490 m. Rocks of the Franciscan Formation, a subduction complex consisting of accreted fragments of oceanic crust and forearc sediments, underlay most of the region (Aalto and Harper 1989). Soils were mapped as predominantly Melbourne and Empire series by the California State Cooperative Soil-Vegetation Survey (Smith et al. 1977; Delapp et al. 1978).

Crescent City, CA is the closest weather station to the study area. Precipitation data (1948–2000) indicated that maximum precipitation fell during December and January, averaging 27.7 cm and 29.6 cm, respectively. The least amount fell during July and August, averaging 1.0 cm and 2.0 cm, respectively. Annual average precipitation was 168.1 cm. The highest mean temperatures occurred in Crescent City during August and September, at 14.9°C and 14.6°C, respectively. The lowest mean temperatures occurred in December and January, at 8.8°C

TABLE 1. COVER ABUNDANCE SCALE AND MIDPOINTS USED IN OCULAR ESTIMATES.

Cover class	Range of cover (%)	Class midpoints (%)
8	75–100	87.5
7	50–75	62.5
6	25–50	37.5
5	5–25	15
4	1–5	3
3	0.1–1	0.6
2	0.01–0.1	0.06
1	0.001–0.01	0.006

and 8.7°C, respectively (Western U.S. Climate Historical Summaries 2000).

Study area vegetation conforms to the Society of American Foresters redwood forest cover type (Eyre 1980). East and north of the study area, the Douglas-fir forest cover type dominates.

Sampling. For Jedediah Smith Redwoods State Park, Del Norte Coast Redwoods State Park, and Redwood National Park, old-growth forest was identified on 1:12,000 color infrared aerial photographs. Two hundred plots were stratified based on three elevation classes (0–105 m, 106–215 m, and >215 m), and placed onto USGS topographic quadrangles in a systematic grid 485 meters apart.

For Siskiyou National Forest, four old-growth polygons were identified on maps obtained from the USDA Forest Service GIS database, and transferred to 1:24,000 USGS topographic quadrangles. Five plots were placed in each polygon via a systematic sampling grid, with plot spacing proportional to polygon area.

Riparian zones within Jedediah Smith Redwoods State Park were sampled separately to best characterize this unique and diverse vegetation. Fifteen sample plots were systematically placed approximately 1500 m apart (total stream length/15) along Cedar Creek, Mill Creek, Clarks Creek, and several other unnamed perennial drainages within park boundaries.

Of 235 plots slated for sampling, 206 were eventually field checked. The remaining plots were not sampled because of difficult or dangerous access, or the plot was not in an old-growth forest. The 206 circular 0.05 ha (500 m^2) plots were thoroughly searched and all vascular plant species identified and recorded with an ocular cover estimate using a modified Braun-Blanquet cover abundance scale (Table 1; Mueller-Dombois and Ellenberg 1974). Tree species were tallied based on stem density in three height classes: 0–3 m, 3–10 m, and >10 m. Basal area, taken from plot center, was estimated using a "cruise angle" sighting device for canopy (dominant, co-dominant, and intermediate crown classes) species. Elevation was determined with a pocket altimeter and topographic map. Slope angle was recorded in percent using a clinometer. Aspect

was assessed with a hand compass. Distance from the ocean was estimated using a topographic map. Topographic position was recorded for each plot.

Data Analysis. Two-Way Indicator Species Analysis (TWINSPAN) (Hill 1979) was used to simultaneously classify species and samples. Only species occurring in greater than 5 percent of plots were used in the analysis (Gauch 1982). Plots were analyzed in TWINSPAN with species cover cut levels of 0.6, 3.0, 15.0, 37.5, 62.5, and 87.5 percent. The 15.0 and 37.5 cut levels were weighted to emphasize dominance (Stuart et al. 1996). TWINSPAN groupings were analyzed using a polar (Bray-Curtis) ordination, to further analyze and refine the TWINSPAN output. Species richness was determined by randomly selecting 5 plots from each association and calculating the mean number of species per plot (Stuart et al. 1996). In addition, stem density per hectare in three height classes and canopy species basal area were averaged for each association.

Discriminant analysis was performed using NCSS 2000 (Hintze 1998) to relate floristic associations with abiotic site characteristics. Elevation, slope angle, coastal proximity, and a Moisture Equivalency Index (MEI) were used as abiotic variables in the discriminant analysis. The MEI was adapted from Sawyer and Thornburgh (1974) and Matthews (1986). It incorporates topographic position and aspect, two variables important to soil moisture. A lower index number (1–15) assumes greater soil moisture available to plants.

RESULTS AND DISCUSSION

TWINSPAN and polar ordination analysis produced six groups that were interpreted as associations (Fig. 1). Groups were consistent with vegetation units observed in the field. All associations were in the *Sequoia sempervirens* series, with *Pseudotsuga menziesii* (Mirbel) Franco, *Tsuga heterophylla* (Raf.) Sarg., and *Alnus rubra* Bong. sub-series. The first TWINSPAN division separated groups based on understories dominated by either *Vaccinium ovatum* Pursh or *Polystichum munitum* (Kaulf) C. Presl. Within these broad groupings, subsequent TWINSPAN division levels reflected groupings based on other indicator understory species such as *Lithocarpus densiflorus* (Hook. & Arn.) Rehder, *Rhododendron macrophyllum* D. Don, and *Rubus spectabilis* Pursh. The following association descriptions are presented from relatively dry types to wet types. A more detailed treatment of the associations can be found in Mahony (1999).

The Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum Association.

Total vegetation cover averaged 85 percent, and total overstory cover averaged 68 percent. Overstories were dominated by *Sequoia sempervirens* and *Pseudotsuga menziesii,* with mean cover values
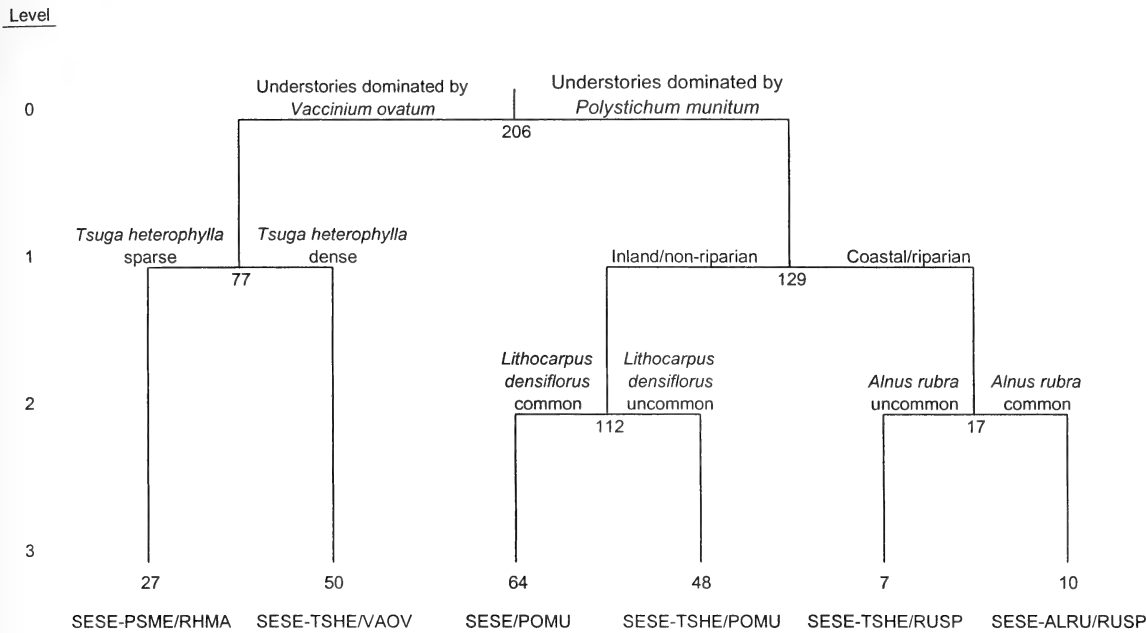
Level

FIG. 1.   Dendrogram of TWINSPAN classification. Numbers beneath lines represent the number of plots prior to division. Numbers above association acronyms are the number of plots in each classified association. Association acronyms are: SESE-PSME/RHMA = *Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum*, SESE-TSHE/VAOV = *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum*, SESE/POMU = *Sequoia sempervirens/Polystichum munitum*, SESE-TSHE/POMU = *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum*, SESE-TSHE/RUSP = *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis*, SESE-ALRU/RUSP = *Sequoia sempervirens-Alnus rubra/Rubus spectabilis*.

of 43 and 31 percent, respectively, and mean constancies of 96 and 100 percent, respectively (Table 2). *Tsuga heterophylla* was occasionally present but contributed minimal cover. *Lithocarpus densiflorus* dominated the sub-canopy. Basal area averaged 123 m²/ha (Table 3).

The shrub layer was extremely dense. *Vaccinium ovatum* and *Rhododendron macrophyllum* dominated, with mean cover values of 47 and 35 percent, respectively, and mean constancies of 100 percent each. *Berberis nervosa* Pursh, *Gaultheria shallon* Pursh, *Rhamnus purshiana* DC., and *Vaccinium parvifolium* Smith each had greater than 30 percent constancy but less than 3 percent cover.

The herb layer was virtually absent. *Polystichum munitum* was the most dominant species in this layer with 7 percent cover and 93 percent constancy. *Disporum hooker* (Torrey) Nicholson, *Galium triflorum* Michaux, *Oxalis oregana* Nutt., *Trillium ovatum* Pursh, and *Viola sempervirens* E. Greene were common but contributed negligible cover.

The *Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum* association was generally found on upper slopes and ridges in Siskiyou National Forest and Del Norte Coast Redwoods State Park. Elevations ranged from 58–470 m, averaging 312 m. Distance from the ocean averaged 8.5 km. Slopes averaged 43 percent, and Moisture Equivalency Index (MEI) scores averaged

9.8. Species richness averaged 13.6 species (Table 4).

Vegetation dynamics. *Lithocarpus densiflorus* and *Sequoia sempervirens* dominated reproduction. Veirs (1979) suggested *S. sempervirens* and *L. densiflorus* were components of the "climax" vegetation and would remain in the stand regardless of disturbance such as fire. The presence of *S. sempervirens* in all height classes represents an uneven age structure for redwood. *Pseudotsuga menziesii* is a seral species that will disappear from stands without major disturbance (Daubenmire 1975; Veirs 1979; Eyre 1980). Low *P. menziesii* stem densities for the 0–3 m and 3–10 m height classes, and high density of trees >10 m, suggested that a cohort resulted from disturbance, and additional disturbance will be necessary for continued presence of *P. menziesii* in this association.

Relationships to previous classifications. The *Sequoia sempervirens-Pseudotsuga menziesii/Rhododendron macrophyllum* association closely resembled the midslope stands encountered by Dyrness et al. (1972) in Wheeler Creek Research Natural Area, and Tanoak-coast redwood association stands described by Atzet and Wheeler (1984) for southwestern Oregon. Other similar types include the *Sequoia sempervirens-Pseudotsuga menziesii/Vaccinium ovatum* association described by Matthews

TABLE 2. AVERAGE COVER AND CONSTANCY FOR SPECIES USED IN TWINSPAN ANALYSIS. Species reported are those with >50 percent constancy. See Figure 1 for plant association acronyms. Cov = average cover (%). Con = constancy (%).

	SESE-PSME/RHMA		SESE-TSHE/VAOV		SESE/POMU		SESE-TSHE/POMU		SESE-TSHE/RUSP		SESE-ALRU/RUSP	
	Cov	Con	Cov	Con	Cov	Con	Cov	Con	Cov	Con	Cov	Con
Maianthemum dilatatum							<1	52				
Menziesia ferruginea							3	69				
Pseudotsuga menziesii	31	100	17	78								
Rhododendron macrophyllum	35	100	13	76								
Viola sempervirens	<1	74	<1	90	<1	61						
Disporum hookeri			<1	54	<1	66						
Lithocarpus densiflorus	45	100	21	94	16	95			8	57		
Vaccinium ovatum	47	100	51	98	16	97	14	98	5	57	2	70
Tsuga heterophylla			41	100	24	75	39	88	21	86		
Trillium ovatum	<1	93	<1	98	<1	98	<1	69	<1	86		
Vaccinium parvifolium	1	70	2	70	3	73	5	94	3	86		
Blechnum spicant			3	72	4	73	11	96	10	100	<1	50
Polystichum munitum	7	93	12	100	55	100	67	100	30	100	24	100
Sequoia sempervirens	43	96	37	100	60	100	53	98	22	86	36	80
Oxalis oregana	<1	52	<1	78	13	98	9	100	16	100		
Disporum smithii							<1	67	<1	100		
Rhamnus purshiana							<1	60	1	57		
Gaultheria shallon	2	78	2	74	5	80	1	75	6	71	10	80
Galium triflorum			<1	54	<1	61			<1	57	<1	60
Vancouveria hexandra					<1	55			<1	57	<1	10
Dryopteris expansa							2	75	1	86	2	50
Rubus spectabilis							5	63	25	100	22	100
Acer circinatum									19	71		
Acer macrophyllum									10	57		
Adiantum aleuticum									<1	71		
Corylus cornuta									14	57		
Ribes bracteosum									1	57		
Asarum caudatum									<1	71	<1	70
Athyrium filix-femina							<1	58	2	100	2	60
Tolmiea menziesii									<1	71	2	60
Alnus rubra											38	100
Claytonia sibirica											<1	80
Marah oreganus											5	80
Polypodium scouleri											<1	50
Rubus parviflorus											3	90
Sambucus racemosa											3	70
Stachys ajugoides											<1	90

(1986) and the *Sequoia sempervirens/Arbutus menziesii* Pursh association described by Lenihan (1986). This association might be considered an extension of the *Pseudotsuga*-hardwood forests described by Sawyer et al. (1977).

The Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum Association.

Total vegetation cover averaged 88 percent, and total overstory cover averaged 74 percent. *Sequoia sempervirens, Tsuga heterophylla,* and *Pseudotsu-*

TABLE 3. MEAN BASAL AREA (M²/HA) FOR CANOPY SPECIES BY ASSOCIATION.

	SESE-PSME/RHMA	SESE-TSHE/VAOV	SESE/POMU	SESE-TSHE/POMU	SESE-TSHE/RUSP	SESE-ALRU/RUSP
Sequoia sempervirens	86.0	114.0	165.0	170.0	73.0	87.0
Pseudotsuga menziesii	37.0	21.0	10.0	2.0	2.0	7.0
Tsuga heterophylla	0.4	23.0	15.0	23.0	11.0	0.0
Picea sitchensis	0.0	0.0	0.0	4.0	6.0	10.0
Abies grandis	0.0	3.0	1.0	0.2	0.0	3.0
Total basal area	123.4	161.0	191.0	199.2	92.0	107.0

TABLE 4. ENVIRONMENTAL CHARACTERISTICS, TREE DENSITY IN THREE HEIGHT CLASSES, AND SPECIES RICHNESS FOR EACH FOREST ASSOCIATION.

	SESE-PSME/RHMA	SESE-TSHE/VAOV	SESE/POMU	SESE-TSHE/POMU	SESE-TSHE/RUSP	SESE-ALRU/RUSP
Elevation (m)	312.0	161.0	143.0	114.0	67.0	136.0
Distance (km)	8.5	7.4	6.4	5.5	6.8	3.6
Slope (%)	42.9	36.2	36.2	34.9	38.0	49.7
MEI (1–15)	9.8	9.0	7.5	7.0	1.3	6.7
Stems/ha:						
0–3 m	71.8	87.6	114.0	54.0	68.6	74.0
3–10 m	127.6	76.8	86.6	66.2	51.6	168.0
>10 m	180.8	206.0	172.4	165.8	72.0	170.0
Sp. Richness	13.6	16.6	19.0	15.6	26.8	19.4

ga menziesii dominated the canopy, with mean covers of 37, 41, and 17 percent, respectively, and mean constancies of 100, 100, and 78 percent, respectively (Table 2). *Abies grandis* (Douglas) Lindley appeared occasionally in the canopy. *Lithocarpus densiflorus* was common in the subcanopy. Basal area averaged 161.0 m²/ha (Table 3).

The shrub layer was dense. *Vaccinium ovatum* dominated, averaging 51 percent cover and 98 percent constancy. *Rhododendron macrophyllum* had 13 percent cover and 76 percent constancy. *Berberis nervosa, Gaultheria shallon* and *Vaccinium parvifolium* each had greater than 40 percent constancy but less than 2 percent cover. *Corylus cornuta* Marsh. and *Rhamnus purshiana* occurred sporadically.

The sparse herb layer was dominated by *Polystichum munitum,* averaging 12 percent cover and 100 percent constancy.

The *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum* association was usually found on inland upper slopes and ridges in Jedediah Smith Redwoods State Park. Elevations ranged from 40–460 m, averaging 161 m. Distance inland averaged 7.4 km. Slopes averaged 36 percent, and MEI scores averaged 9. Species richness averaged 16.6 species (Table 4).

Vegetation dynamics. Tsuga heterophylla and *Lithocarpus densiflorus* dominated reproduction. *Tsuga heterophylla* seedlings were particularly abundant on downed logs. Combs (1984) noted a similar pattern of *T. heterophylla* regeneration in the Little Lost Man Creek Research Natural Area in Redwood National Park. He suggested that few seedlings would reach maturity because of vulnerability to fire and disease. Daubenmire (1975) noted extensive *T. heterophylla* in all size classes in Jedediah Smith Redwoods State Park, but believed the species would decline without disturbance. Veirs (1979) suggested that light ground fires, unaffecting the canopy, will favor *T. heterophylla* regeneration. The high density of *T. heterophylla* and the complete absence of *P. menziesii* seedlings suggested a light fire regime, sufficient for *S. semper-*

virens and *T. heterophylla* regeneration, but not for regeneration of *P. menziesii.*

Relationships to previous classifications. The *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum* association was unique compared to other redwood types described in the literature due to the importance of *Tsuga heterophylla.* While other redwood classifications have noted the presence of *T. heterophylla* (Dyrness et al. 1972; Atzet and Wheeler 1984; Lenihan 1986), none have shown such dominance by this mesic conifer. The *Sequoia sempervirens/Berberis nervosa* association described by Lenihan (1986), and the *Tsuga* phase of the *Pseudotsuga*-hardwood forests described by Sawyer et al. (1977) were similar in composition to this association.

The Sequoia sempervirens/Polystichum munitum Association.

Total vegetation cover averaged 90 percent. Total overstory cover averaged 76 percent. *Sequoia sempervirens* dominated the canopy with 60 percent cover and 100 percent constancy (Table 2). *Tsuga heterophylla* was common, and *Pseudotsuga menziesii* appeared occasionally in the canopy. *Abies grandis, Cupressus lawsoniana* A. Murray and *Umbellularia californica* (Hook. & Arn.) Nutt. occurred sporadically, contributing minimal cover. *Lithocarpus densiflorus* was ubiquitous in the subcanopy. Basal area averaged 191.0 m²/ha (Table 3).

Vaccinium ovatum dominated the relatively sparse shrub layer, averaging 16 percent cover and 97 percent constancy. *Gaultheria shallon, Rhododendron macrophyllum,* and *Vaccinium parvifolium* each had greater than 40 percent constancy but less than 5 percent cover. *Acer circinatum* Pursh, *Berberis nervosa, Corylus cornuta,* and *Rubus spectabilis* occurred sporadically, contributing minimal cover.

Herbaceous cover and species diversity was moderately high. *Polystichum munitum* dominated, averaging 55 percent cover and 100 percent constancy. *Oxalis oregana* was extremely common.

The *Sequoia sempervirens/Polystichum munitum*

association was found throughout the study area, generally on lower and middle slopes at moderate distances from the ocean. Elevations ranged from 21–369 m, averaging 143 m. Distance from the ocean averaged 6.4 km. Slopes averaged 36 percent, and MEI scores averaged 7.5. Species richness averaged 19 species (Table 4).

Vegetation Dynamics. Lithocarpus densiflorus and *Sequoia sempervirens* dominated reproduction. The moderate levels of *Abies grandis, Tsuga heterophylla,* and *L. densiflorus* reproduction may be indicative of the light fire regime in intermediate to mesic sites referred to by Veirs (1979). However, he noted that these species exhibited an all aged pattern and can reproduce regardless of fire.

Relationships to previous classifications. The *Sequoia sempervirens/Polystichum munitum* association contained elements of the *Sequoia sempervirens/Blechnum spicant* (L.) Smith association described by Lenihan (1986), though Lenihan's association appeared wetter. The dominance of *Sequoia sempervirens,* the sparse shrub layer, and the well-developed herb layer related this association to Becking's (1967) Redwood-oxalis alliance.

The Sequoia sempervirens-Tsuga heterophylla/ Polystichum munitum Association.

Total vegetation cover averaged 92 percent, and total overstory cover averaged 75 percent. *Sequoia sempervirens* and *Tsuga heterophylla* dominated the canopy, with mean covers of 53 and 39 percent, respectively, and mean constancies of 98 and 88 percent, respectively (Table 2). *Abies grandis, Lithocarpus densiflorus, Picea sitchensis* (Borg.) Carrière and *Pseudotsuga menziesii* occurred sporadically, contributing minimal cover. *Thuja plicata* D. Don appeared occasionally in mesic sites. Basal area averaged 199.2 m²/ha (Table 3).

The shrub layer was generally not well developed. *Vaccinium ovatum* was the most abundant shrub, averaging 14 percent cover and 98 percent constancy. *Menziesia ferruginea* Smith, *Rubus spectabilis, Vaccinium parvifolium, Gaultheria shallon,* and *Rhamnus purshiana* each had greater than 60 percent constancy but less than 6 percent cover.

The herbaceous layer was dense. *Polystichum munitum* dominated, averaging 67 percent cover and 100 percent constancy. *Blechnum spicant* and *Oxalis oregana* were common.

The *Sequoia sempervirens-Tsuga heterophylla/ Polystichum munitum* association was generally found at lower slopes and elevations, especially in southwestern areas of Jedediah Smith Redwoods State Park exposed to maritime influence. Elevations ranged from 40–274 m, averaging 114 m. Distance inland averaged 5.5 km. Slopes averaged 35 percent, and MEI scores averaged 7. Species richness averaged 15.6 species (Table 4).

Vegetation Dynamics. Tsuga heterophylla and *Sequoia sempervirens* dominated reproduction. Se-

quoia sempervirens had fewer stems in the lower height classes relative to *T. heterophylla,* but the longevity and resilience of *S. sempervirens* makes abundant individuals in the reproduction layers unnecessary to ensure continued dominance.

Relationships to previous classifications. The *Sequoia sempervirens-Tsuga heterophylla/Polystichum munitum* association, like *Sequoia sempervirens-Tsuga heterophylla/Vaccinium ovatum,* appeared unlike any previously described redwood types. It was similar in many respects to the mesic *Tsuga/Polystichum* association described by Franklin and Dyrness (1973) for Oregon Coast Range forests in the *Tsuga heterophylla* Zone. Additionally, it contained elements of the *Tsuga-picea/Oplopanax horridum/Athyrium filix-femina* association of *Picea sitchensis* Zone forests described by Franklin and Dyrness (1973). It related tangentially to Lenihan's (1986) *Sequoia sempervirens/Blechnum spicant* association.

The Sequoia sempervirens-Tsuga heterophylla/ Rubus spectabilis Association.

Total vegetation cover averaged 94 percent, and total overstory cover averaged 55 percent. *Sequoia sempervirens* and *Tsuga heterophylla* were canopy dominants, averaging 22 and 21 percent cover, respectively. Both species had 86 percent constancy (Table 2). *Picea sitchensis* and *Thuja plicata* were occasional to common in mesic sites. *Pseudotsuga menziesii* occurred sporadically. *Acer macrophyllum* was common, especially near stream channels. *Lithocarpus densiflorus* was common in the subcanopy. *Alnus rubra* and *Sambucus racemosa* L. appeared occasionally. Basal area averaged 92.0 m²/ha (Table 3).

Rubus spectabilis dominated the dense shrub layer, averaging 25 percent cover and 100 percent constancy. *Acer circinatum* and *Corylus cornuta* were abundant in this layer having 71 percent and 57 percent constancy and 19 percent and 14 percent cover, respectively. Other common shrubs having greater than 40 percent constancy but less than 6 percent cover included *Gaultheria shallon, Menziesia ferruginea, Rhamnus purshiana, Ribes bracteosum* Douglas, *Rubus parviflorus, Vaccinium ovatum,* and *V. parvifolium.*

The herbaceous layer was dense and floristically diverse. *Polystichum munitum* dominated with 31 percent cover and 100 percent constancy. *Oxalis oregana* and *Blechnum spicant* were abundant.

The *Sequoia sempervirens-Tsuga heterophylla/ Rubus spectabilis* association was restricted to interior perennial drainages in Jedediah Smith Redwoods State Park. Elevations ranged from 37–122 m, averaging 67 m. Distance from the ocean averaged 6.8 km. Slopes averaged 38 percent, and MEI scores averaged 1.3. Species richness averaged 26.8 species (Table 4).

Vegetation Dynamics. Tsuga heterophylla and *Lithocarpus densiflorus* dominated reproduction.

TABLE 5. STANDARD CANONICAL COEFFICIENTS USED IN DISCRIMINANT ANALYSIS.

Variable	Variate 1	Variate 2	Variate 3	Variate 4
Elevation	−0.874009	0.717388	0.045912	−0.376631
Slope	0.189664	0.275203	0.477507	0.858742
Distance	−0.828487	−0.300679	−0.599034	0.465420
MEI	−0.376680	−1.100974	0.339726	0.143424

Riparian conditions produced the wettest and most floristically diverse association encountered in the study area. Conifer basal area was greatly reduced compared to other associations. *Sequoia sempervirens* attained its lowest basal area, but still dominated conifer basal area. The streamside environment allowed mesic woody species such as *Acer macrophyllum, A. circinatum, Corylus cornuta,* and *Rubus spectabilis* to thrive.

Relationships to previous classifications. The *Sequoia sempervirens-Tsuga heterophylla/Rubus spectabilis* association appeared much wetter than any redwood association previously described. It shared many of the same riparian components, such as high cover of herbaceous and hardwood species, described by Dyrness et al. (1972) for lower slopes in the Wheeler Creek Research Natural Area in southwestern Oregon, and appeared similar in many respects to the *Tsuga heterophylla/Acer circinatum/Polystichum munitum-Oxalis oregana* association described by Franklin and Dyrness (1973) for alluvial terrace vegetation in the *Tsuga heterophylla* Zone of Oregon. The absence of *Sequoia sempervirens* in *Tsuga heterophylla* Zone forests makes comparison difficult, however.

The Sequoia sempervirens-Alnus rubra/Rubus spectabilis Association.
Total vegetation cover averaged 93 percent, and total overstory cover averaged 71 percent. *Sequoia sempervirens* dominated the canopy, averaging 36 percent cover and 80 percent constancy (Table 2). *Picea sitchensis* was common in coastal sites. *Pseudotsuga menziesii* and *Abies grandis* occurred sporadically. *Alnus rubra* dominated the subcanopy. *Acer macrophyllum, Lithocarpus densiflorus, Rhamnus purshiana, Sambucus racemosa,* and *Umbellularia californica* appeared occasionally in the subcanopy. Basal area averaged 107.0 m²/ha (Table 3).
Rubus spectabilis dominated the moderately dense shrub layer, averaging 22 percent cover and 100 percent constancy. *Gaultheria shallon* had 10 percent cover and 80 percent constancy. Other common shrubs included *Acer circinatum, Corylus cornuta, Rubus parviflorus, R. ursinus* Cham & Schldl., and *Vaccinium ovatum* with constancies greater than 20 percent but with less than 8 percent cover.
The herbaceous layer was diverse. *Polystichum munitum* dominated, averaging 24 percent cover and 100 percent constancy. *Oxalis oregana* oc-

curred sporadically, but was generally abundant when it did occur.
The *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* association was generally found along the Smith River, or on coastal bluffs in Del Norte Coast Redwoods State Park. Elevations ranged from 18–299 m, averaging 136 m. Distance from the ocean averaged 3.6 km. Slopes averaged 50 percent, and MEI scores averaged 6.7. Species richness averaged 19.4 species (Table 4).

Vegetation dynamics. Sequoia sempervirens dominated reproduction. *Picea sitchensis* was very common on coastal bluffs, and *Pseudotsuga menziesii* was common along the Smith River. *Alnus rubra* achieved high cover in the subcanopy. The mesic, high light environments of the Smith River floodplain and exposed coastal bluffs provided favorable conditions for this shade intolerant hardwood (Hibbs et al. 1994; Harlow et al. 1996). Additionally, natural disturbance from Smith River flooding likely enhanced the competitive ability of *A. rubra,* which is more tolerant of flooding and poor drainage than its associates (Hibbs et al. 1994). Tolerance of salt spray and resistance to windthrow allowed *A. rubra* to thrive along the coastal bluffs of Del Norte Coast Redwoods State Park. Periodic disturbances likely benefited the seral *Pseudotsuga menziesii. Alnus rubra* showed high stem densities in the 3–10 and >10 m height classes, but minimal density in the 0–3 m class, indicating many stands may be recovering from disturbance.

Relationships to previous classifications. The *Sequoia sempervirens-Alnus rubra/Rubus spectabilis* association was similar to coastal sections of the Wildcat Hills transect described by Zinke (1977), as well as the red alder series described in Sawyer and Keeler-Wolf (1995). It should be noted that a pure *Picea sitchensis* forest type may exist immediately adjacent to the coast in Del Norte Coast Redwoods, but was not sampled.

Discriminant Analysis. Discriminant analysis revealed that elevation, coastal proximity, and topographic position/aspect (MEI) were statistically significant (P < 0.01) in discriminating among floristic associations. Elevation and coastal proximity had the greatest influence on the first discriminant function (Table 5). This function explained 81.1 percent of the variation between groups. MEI had the greatest influence on the second discriminant function,

which explained 14.2 percent of group variation. Together, the first two discriminant functions, influenced by elevation, distance to the ocean, and MEI, explained 95.3 percent of group variation. The physiographic factors influencing floristic associations, in decreasing order of importance, were elevation, coastal proximity, and aspect/topographic position (MEI).

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ESTIMATED AGES OF SOME LARGE GIANT SEQUOIAS: GENERAL SHERMAN KEEPS GETTING YOUNGER

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ABSTRACT

Using a method that combines information on tree size with growth rates determined from relatively short increment cores, I estimated the ages of several of the largest living *Sequoiadendron giganteum* (Lindley) Buchholz. Compared to the longest-lived *S. giganteum* known, which was at least 3266 years old, most of the large sequoias analyzed here were relatively young, with estimated ages of only 1650 to 2150 years. Thus, contrary to common supposition, the largest *S. giganteum* generally owe their great size to rapid growth, not to exceptional age. However, two of the largest *S. giganteum* were substantially older, with estimated ages of 2850 and 2890 years. There is a high probability that some *S. giganteum* living today are older than the oldest *S. giganteum* yet discovered.

People have long been fascinated by the great size and longevity of *Sequoiadendron giganteum* (Lindley) Buchholz (giant sequoias), which grow naturally only in isolated groves on the western slope of California's Sierra Nevada. *Sequoiadendron giganteum* are the world's largest trees, reaching a maximum known bole volume of nearly 1500 m^3 (Hartesveldt et al. 1975; Flint 1987 and in press). Precise cross-dating of tree rings on cut stumps has shown that sequoias can reach at least 3266 years in age (R. Touchan personal communication), making *S. giganteum* the third longest-lived, non-clonal tree species known, exceeded only by *Pinus longaeva* Bailey (bristlecone pine, 4844 years) of western North America's Great Basin (Currey 1965) and *Fitzroya cupressoides* (Molina) Johnston, (alerce, 3613 years) of Chile and Argentina (Lara and Villalba 1993).

Here I present age estimates for some large, well-known *S. giganteum*, thereby addressing one of the most frequently-asked questions about famous *S. giganteum*—namely, "how old is this tree?" I additionally address two questions regarding *S. giganteum* sizes and ages. First, are the largest *S. giganteum* so massive because they are exceptionally old, as is often presumed, or because they have grown particularly rapidly? Second, are there likely to be any *S. giganteum* alive today that are older than the longest-lived *S. giganteum* yet known, which is known only from a cut stump?

These questions are difficult to answer because the only way to precisely determine the age of living *S. giganteum* is to crossdate tree rings on increment cores that intersect the tree's pith (Stokes and Smiley 1968). However, the tremendous girth of large *S. giganteum* usually makes it impossible to reach their piths with hand-driven increment borers. Power increment borers with very long bits can sometimes be used to obtain cores that reach the pith (Echols 1969; Johansen 1987), but have several disadvantages, which include unacceptably large holes left in the trees, poor quality of many of the cores extracted, and unacceptable use of noisy power tools on and around popular and frequently-visited *S. giganteum*.

I therefore estimated the ages of several large *S. giganteum* using a method that takes advantage of information from partial increment cores (cores that fall well short of a tree's pith). The derivation and testing of the method is described in detail elsewhere (Stephenson and Demetry 1995). Unlike previous attempts to estimate the ages of large *S. giganteum* (e.g., Douglass 1946; Hartesveldt et al. 1975), this method has been tested on hundreds of *S. giganteum* stumps, does not systematically over- or underestimate tree ages, and offers confidence intervals on the final age estimates.

METHODS

Choice of individual Sequoiadendron giganteum *for analysis.* The primary criteria for choosing individual *S. giganteum* for analysis were (1) the *S. giganteum* were among the largest known, and (2) the cores and other data needed for age estimation were already available (that is, no *S. giganteum* was to be cored solely for the purpose of this study). Specifically, for a given *S. giganteum* to be included, original increment cores or the necessary measurements from those cores had to be available, along with measurements of the tree's bark thickness and diameter at the height at which the cores were taken. These data requirements limited the pool of *S. giganteum* available for analysis. While many large *S. giganteum* have been cored for studies of human impacts (Hartesveldt 1962, 1965), ring-width chronology development (Brown et al. 1992; Hughes et al. 1996), climatic reconstructions (Hughes and Brown 1992), forest dynamics studies

TABLE 1. *SEQUOIODENDRON GIGANTEUM* SELECTED FOR ANALYSIS (SIZE RANKS AND BOLE VOLUMES ARE FROM FLINT IN PRESS AND PERSONAL COMMUNICATION).

Tree name	Size rank (by volume)	Bole volume (m³)	Location
General Sherman	1	1487	Giant Forest, Sequoia National Park
Washington	2	1355	Giant Forest, Sequoia National Park
General Grant	3	1320	General Grant Grove, Kings Canyon National Park
Boole	7	1202	Converse Basin Grove, Giant Sequoia National Monument
Grizzly Giant	27	963	Mariposa Grove, Yosemite National Park
Cleveland	36	887	Giant Forest, Sequoia National Park
Sentinel	Not ranked	790	Giant Forest, Sequoia National Park

NOTE: Future discoveries of previously unrecognized large sequoias will probably change the ranking of sequoias smaller than the Boole tree. For example, the fourteenth largest sequoia known (the Ishi Giant of Kennedy Grove) was identified only in 1993 (Willard 1994; Flint personal communication).

(Stephenson 1994), and fire history reconstruction (Swetnam 1993), only a limited subset of those *S. giganteum* have associated records of diameter at core height. Diameter at core height is essential for age estimation (Stephenson and Demetry 1995), and cannot be estimated readily from published diameters at breast height of individual *S. giganteum*. Cores are rarely taken exactly at breast height, and sequoia bole diameter usually changes rapidly with increasing distance from breast height.

The following seven large *S. giganteum* were selected for analysis (Table 1). The General Sherman, Washington, and General Grant trees are the world's three largest trees, with the General Sherman and General Grant trees being among the most heavily visited of all *S. giganteum*. The Boole tree is the seventh largest, and is well-known as being the largest sequoia on lands managed by the U.S. Forest Service. The Grizzly Giant is heavily visited because of its craggy appearance and status as one of the two largest *S. giganteum* in Yosemite National Park, whereas the Cleveland tree is a lesser-known and seldom-visited tree in Sequoia National Park. Finally, the Sentinel tree is a well-known sequoia beside the road at the southern entrance to Giant Forest in Sequoia National Park.

The General Sherman, Washington, General Grant, Grizzly Giant, and Cleveland trees all were cored by R. J. Hartesveldt and his colleagues for various studies during the late 1950's and early 1960's. All cores and data sheets for these trees are archived at Sequoia National Park, except I was unable to locate the original core for the Washington tree, and therefore relied exclusively on Hartesveldt's ring measurements for that tree. The Boole tree was cored by researchers from the University of Arizona in 1992; those data were kindly supplied by L. S. Mutch. Finally, the Sentinel tree was cored by V. G. Pile and me in 1998 at the request of National Park Service staff, who wished to have an age estimate for displays near the tree.

Estimating tree ages. I estimated ages of these seven *S. giganteum* following Stephenson and De-

metry's (1995) approach, which combines knowledge of tree size with information gained from partial increment cores. The derivation and biological basis of this approach are too lengthy to repeat here; interested readers are therefore referred to Stephenson and Demetry (1995). When tested on 231 sequoia stumps up to 3200 years old and 6.5 m in diameter, this approach gave age estimates that were within 10% of actual age 62% of the time, and within 25% of actual age 98% of the time, assuming that two 60-cm increment cores are available for analysis; fewer or shorter cores gave less precise estimates. This level of precision is a substantial improvement over that of previously published methods, which estimated tree age from diameter alone, by assuming that basal area increment is constant through time, or by linear extrapolation of growth rates from the innermost portion of an increment core (Stephenson and Demetry 1995).

Sequoia age in years, a, was estimated according to the following equation,

$$a = (c - 100) + \frac{100r^d}{r^d - (r - g)^d} \qquad [1]$$

where c is the full ring count of a partial increment core; g is the length of the innermost 100 rings of the increment core; r is the length g plus the length of the section of bole radius (extending to the tree's pith) that was not sampled by the increment core; and d is given by the following equation:

$$d = 0.230 + 0.759(100/g_{mm}) + 1.27r - 0.848r^2 + 0.159r^3 \qquad [2]$$

Units for g and r are meters, whereas g_{mm} is the length of the innermost 100 rings of the increment core in mm. For reasons discussed in Stephenson and Demetry (1995), if r exceeded 3 m, $r = 3$ m was substituted into eq. 2 for calculating d.

A sequoia's pith usually is not at the geometric center of its bole. However, we typically have no way of determining the location of a living tree's pith, and therefore cannot directly measure the val-

TABLE 2. CONFIDENCE INTERVALS FOR *S. GIGANTEUM* AGE ESTIMATES BASED ON DIFFERENT NUMBERS AND LENGTHS OF INCREMENT CORES (FROM STEPHENSON AND DEMETRY 1995).

	Two 60-cm cores	One 60-cm core	Two 30-cm cores	One 30-cm core
50% confidence interval	−6.9 to 9.0	−8.4 to 9.4	−14.1 to 11.1	−13.0 to 11.8
95% confidence interval	−23.7 to 19.5	−36.7 to 19.7	−45.8 to 26.4	−48.2 to 27.5

NOTE: The intervals are expressed as percentage of estimated sequoia age. For example, the −23.7% listed as one endpoint of the 95% confidence interval for two 60-cm cores means that 2.5% of the time, actual tree age will be more than 1.237 times estimated tree age. (Rephrased, 2.5% of the time estimated sequoia age will be at least 23.7% less, expressed in terms of estimated sequoia age, than actual sequoia age.) The 19.5% listed as the other endpoint of the interval means that 2.5% of the time, actual tree age will be less than 0.805 times estimated tree age.

ue of r associated with a particular increment core. Therefore r was estimated as described by Stephenson and Demetry (1995). First, tree radius was calculated as half of tree diameter (determined by diameter tape) at the height at which the increment core was taken. Average bark thickness, determined by probes at several location around the bole, was then subtracted to determine tree radius inside the bark. From this, the length of the increment core, excluding the core's innermost 100 rings, was subtracted, yielding an estimate of r.

Because increment cores shrink as they dry, the wet length of a core must be known for the most accurate application of eqs 1 and 2. However, for most of the *S. giganteum* analyzed here (the Sentinel tree being the one exception), wet lengths of cores were not recorded. My colleagues and I (unpublished data) have found that the average shrinkage of hundreds of sequoia cores was about 2%. Thus, when the wet length of a core was not recorded, it was estimated by multiplying the core's dry length by 1.02.

To improve accuracy, when several cores were available from a sequoia, a given core's location on the bole had to be separated from that of the other cores by at least 90° of circumference to be included in the age estimation (Stephenson and Demetry 1995). Tree age at height cored was estimated by averaging the age estimates based on the individual cores (Stephenson and Demetry 1995).

Some of the data used to estimate sequoia ages came from *S. giganteum* cored several decades ago. It was therefore necessary to account for the number of years that have passed since a sequoia was cored. Because, for convenience, I wished to estimate all sequoia ages relative to the year 2000, I subtracted the year in which a core was taken from 2000, then added the result to estimated tree age.

The method outlined above only estimates sequoia age at the height at which the cores were taken. However, accounting for the time it took a tree to grow to the height cored potentially can add decades to the tree's estimated age. To account for height growth, I multiplied the height of the core above ground level (in m) by $178x^{-0.957}$, where x is the (estimated) cumulative width, in mm, of the 10 rings that abut the tree's pith. This empirical factor scales height growth to radial growth, and was derived from ring measurements of 41 smaller *S. giganteum* which my colleagues and I cored to the pith both near ground level and near breast height (see Agee et al. 1986 for a similar approach). However, because there is no way of knowing the actual cumulative width of the 10 rings that abut the pith of the large *S. giganteum* analyzed here, I assumed that the width was 27.5 mm, based on the average from measurements of more than 450 sequoia stumps (Table A in Huntington 1914). Thus, I assumed that large *S. giganteum* took $178 \times (27.5)^{-0.957} = 7.5$ years to grow each meter taller until core height was reached. However, with the exception of the Sentinel and Grizzly Giant trees, core heights were not recorded. I therefore estimated core heights for the other trees based on conversations and correspondence with individuals involved in the corings (H. S. Shellhammer for the General Sherman, Washington, General Grant, and Cleveland trees, and R. Adams and L. Mutch for the Boole tree).

Confidence intervals. Stephenson and Demetry (1995) showed that as both the number and length of increment cores increase, confidence in sequoia age estimates also increases (Table 2). However, the numbers and lengths of cores used did not always fall neatly into the categories in Table 2. To determine confidence intervals, core lengths were therefore rounded to the nearest category shown in Table 2 (either 30 or 60 cm). In two cases (the General Sherman and General Grant trees), three cores rather than two were used. However, since confidence is improved relatively little by increasing core number (it is improved more by increasing core length; Table 2), confidence intervals for only two cores were used.

The number of years elapsed between the year in which a tree was cored and the year 2000 was then added to the endpoints of the tree's confidence intervals, as was the estimated number of years it took each sequoia to grow to the height at which it was cored. Admittedly, the latter step does not change a sequoia's age confidence intervals to reflect the uncertainty associated with estimating the number of years it took a sequoia to grow to the height cored. However, uncertainty added at this

TABLE 3. DATA USED TO ESTIMATE THE AGES OF THE SELECTED *S. GIGANTEUM*. [a] Side of tree from which core was taken. [b] Confidence intervals (see Table 2) are: 1 × 30, one 30-cm increment core; 2 × 30, two 30-cm cores; 1 × 60, one 60-cm core; 2 × 60, two 60-cm cores. [c] Estimated from length of innermost 154 rings. [d] Estimated from length of innermost 280 rings.

Tree	Core[a]	Diameter at core height (m)	Bark thick-ness (m)	Wet length of full core (m)	Wet length of innermost 100 rings of core (m)	Ring count of full core	Height of core above ground (m)	Year cored	Confidence interval used[b]
General Sherman	South	7.325	0.127	0.387	0.148	317	1.6	1964	2 × 30
	Northwest	7.325	0.127	0.365	0.156	249	1.6	1964	
	East	7.325	0.127	0.352	0.120	315	1.6	1964	
Washington	—	7.858	0.152	0.291	0.091	325	1.4	1963	1 × 30
General Grant	Southeast	6.705	0.203	0.375	0.259	146	2.0	1964	2 × 30
	West	6.705	0.203	0.376	0.180	233	2.0	1964	
	North	6.705	0.203	0.378	0.139	293	2.0	1964	
Boole	B (Northwest?)	7.45	0.090	0.418	0.124[c]	259	1.4	1992	1 × 60
	C (Northeast?)	7.45	0.090	0.639	0.159[d]	386	1.4	1992	
Grizzly Giant	Southwest	6.621	0.127	0.289	0.175	206	3.05	1958	2 × 30
	East	6.621	0.127	0.266	0.148	175	3.05	1958	
Cleveland	—	5.613	0.127	0.347	0.045	598	1.6	1964	1 × 30
Sentinel	Northeast	6.399	0.073	0.515	0.099	366	2.56	1998	2 × 60
	Southwest	6.399	0.073	0.556	0.128	333	2.04	1998	

stage is small compared to the uncertainty of estimating the tree's age at core height.

Statistics on the longest-lived sequoia known. As a yardstick for interpreting results, I used the age and size of the longest-lived sequoia known—a cut stump in Converse Basin, Giant Sequoia National Monument, designated CBR26 by its discoverers (R. Touchan and E. Wright of the University of Arizona's Laboratory of Tree-Ring Research). To-
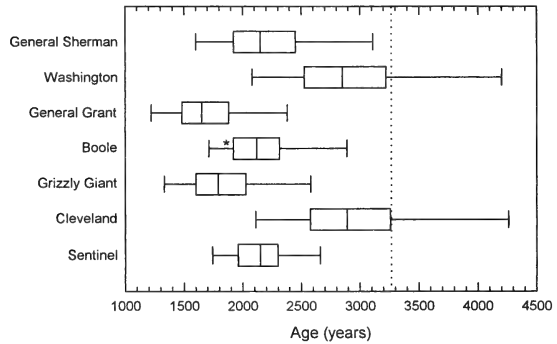

FIG. 1. Estimated ages of selected *S. giganteum* in the year 2000, with associated confidence intervals. The vertical line within each horizontal box indicates that tree's estimated age. The ends of each box delimit the 50% confidence interval for that tree's age, whereas the "whiskers" extending from each box delimit the 95% confidence interval. The dotted vertical line at 3266 years indicates the age of the oldest sequoia yet discovered (see the text). Because the innermost ring of a long core taken within a fire scar cavity at the base of the Boole tree has been crossdated to A.D. 143 by E. Wright of the University of Arizona (L. Mutch personal communication), the Boole tree is at least 1858 years old, as indicated by the asterisk.

uchan has precisely crossdated 3207 rings on the stump. It is missing much of its sapwood, so the outermost ring dates to 1834. However, the extensive logging of Converse Basin Grove occurred between 1893 and 1908 (Johnston 1983; Willard 1994). Thus, at least 59 years of sapwood are missing, and the tree therefore was at least 3266 years old when it was cut. (It is unlikely that the tree exceeded 3290 years old, including the time it took the tree to grow to the height sampled by Touchan and Wright.) The stump is relatively small: 5.8 m in diameter near ground level and 4.3 m in diameter at the cut surface 2.2 m above ground level (R. Touchan personal communication). Even with sapwood and bark intact, the tree's diameter at 2.2 m above ground level was probably less than 5 m when it was cut, much smaller than any of the trees analyzed here (Table 3). While we will never know the volume of the living CBR26, it is clear that many hundreds of *S. giganteum* alive today (probably well over one thousand) are larger than CBR26 was before it was cut (e.g., see Appendix 1 in Stohlgren 1991).

RESULTS

Table 3 presents the data used to estimate the ages of the seven large *S. giganteum*. Estimated ages ranged from 1650 years for the General Grant tree to 2890 years for the Cleveland tree (Fig. 1), averaging 2230 years. Though all of these *S. giganteum* were much larger than CBR26, the longest-lived sequoia known, five had estimated ages at least 1000 years younger than CBR26 (Fig. 1). In fact, the third-largest living sequoia (the General Grant tree) is estimated to be little more than half

as old as CBR26. Additionally, CBR26's age lies well outside of the high end of the 95% confidence intervals of the five *S. giganteum* (Fig. 1).

While there are exceptions (namely, the Washington and Cleveland trees), the largest living *S. giganteum* generally owe their great bulk to rapid growth, not to extraordinary age. For example, average ring width from the cores of the (estimated) youngest sequoia (the General Grant tree, 1.82 mm) was more than three times that of the (estimated) oldest sequoia (the Cleveland tree, 0.58 mm). This notion is further supported by Huntington's (1914) age data from more than 450 sequoia stumps (the accuracy of which is discussed in Stephenson and Demetry 1995). Huntington's ten largest stumps averaged 6.0 m in diameter inside the bark, but only 1842 years old by direct ring count (the largest was 6.5 m in diameter but only 1347 years old). In sharp contrast, his ten oldest stumps averaged only 4.9 m in diameter inside the bark, but 2822 years old—1 m less in diameter but nearly 1000 years older. Membership in the two groups of stumps was almost mutually exclusive; only one stump was both one of the ten largest and one of the ten oldest (see Fig. 1 in Stephenson and Demetry 1995). Thus, for whatever reason, *S. giganteum* that reach great age tend to have grown relatively slowly.

Figure 1 indicates that there is a 25% probability that the Cleveland tree is older than CBR26, and a similar probability that the Washington tree is older. The probability that at least one of these two living trees (Cleveland or Washington) is older than CBR26 therefore is roughly $1 - (0.75)^2$, or 44%—nearly even odds. Given that the seven *S. giganteum* examined here are only a small sample of all potentially old, living *S. giganteum* (likely candidates would number well over one thousand), it seems highly likely that some *S. giganteum* living today exceed the age of CBR26.

DISCUSSION

There has been a long-standing belief that the largest *S. giganteum* are the oldest. This is well illustrated by tracing the history of age estimates for the General Sherman tree, the world's largest tree. By the early 20th century, careful ring counts and crossdating had identified a handful of sequoia stumps more than 3000 years old, the oldest being about 3200 years old (Huntington 1914; Douglass 1919, 1945). (John Muir's reported count of 4000 rings on the "Muir Snag" in 1875 has not been repeated and was almost certainly in error [Flint 1987], and other early claims of up to 11,000 rings counted on stump tops [Jordan 1907] cannot be taken seriously.) Since none of these old stumps approached the great size of the General Sherman tree, most natural historians concluded that the General Sherman tree must be more than 3500 years old (e.g., Fry and White 1930). Stewart (1930) believed that the General Sherman tree was

about 4000 years old, though he reported that an estimate based on "average number of rings counted . . . in charred fragments from parts of the [General Sherman tree's] burned trunk, in connection with the actual counts of rings of felled trees . . . which have grown under conditions and situation similar to those of the Sherman tree" yielded an age of 5200 years. Popular publications, such as a 1931 program for a play performed among the sequoias not far from the General Sherman tree, tended to be more extravagant, proclaiming the tree to be 6000 years old (see also Hartesveldt et al. 1975). Ironically, the aforementioned play took place less than two months before the first quantitative estimate of the General Sherman tree's age based on increment cores, by A. E. Douglass.

Douglass, the founder of the modern science of dendrochronology, obtained six short cores from the General Sherman tree in 1931 (the year is mistakenly given as 1935 in Douglass [1946]). He deemed two of the cores to be good enough to use for age estimation, finding that average ring width at 4.6 m above ground level was 0.81 mm. This ring width is less than that of Hartesveldt's cores (Table 3) because it comes from a height where the General Sherman tree's bole is narrower. Douglass stated that "[t]hese are ring sizes which, in relation to the total size of the tree and the probable rate at which rings increase in size toward the center, supplied an estimate of the age of the tree of 3500 years plus or minus 500 years" (Douglass 1946). I have found no quantitative description of how Douglass accounted for "the probable rate at which rings increase in size toward the [tree's] center."

To shed light on Douglass' age estimate, I applied the approach outlined in this paper to his data. Douglass' data yield an age of only 2380 years for the General Sherman tree in 1931, or 2450 years in 2000 (rounded to the nearest decade). This latter estimate is only 300 years older than the estimate based on Hartesveldt's cores (Fig. 1), and is well within that estimate's 95% confidence interval. However, I judge the estimate based on Hartesveldt's cores to be much more reliable than that based on Douglass' cores. Specifically, the estimate based on Hartesveldt's cores required that fewer key parameters be estimated (such as the diameter of the General Sherman tree at 4.6 m above ground level in 1931, needed for using Douglass' data), and was based on three cores widely spaced around the tree's bole, each of which was nearly twice as long as the longest of Douglass' two adjacent cores.

In contrast, an age estimate based on linear extrapolation of Douglass' ring-width data, assuming no change in ring width toward the General Sherman tree's center (an unrealistic assumption), would yield an age of 3790 years in 1931. Thus, Douglass' estimate of 3500 (±500) years apparently was little different from an estimate based on a simple linear extrapolation, and did not adequately consider the increase in ring widths toward the pith.

Douglass' age estimate was widely quoted (and sometimes exaggerated) from 1931 until the 1960's, when Hartesveldt et al. (1975) radically revised the estimate downward. Unlike Douglass, Hartesveldt and his colleagues explicitly stated their assumption as to how ring widths change within a tree: they assumed that basal area increment is constant (that is, trees add a constant amount of basal area each year). This is equivalent to substituting $d = 2$ into eq. 1 (Stephenson and Demetry 1995). Hartesveldt's notes (archived at Sequoia National Park) show that when he strictly adhered to this assumption, he estimated that in 1964 the General Sherman tree was only about 1600 years old. However, Hartesveldt's examination of growth patterns on sequoia stumps measured by Huntington (1914) indicated that strict adherence to this assumption sometimes underestimated the ages of S. giganteum (Hartesveldt et al. 1975). Thus, apparently based on a combination of assumed constant basal area increment and judicious comparisons with Huntington's data, Hartesveldt and his colleagues (1975) cautiously stated that the General Sherman tree ". . . is less than 2500 years old." According to my calculations using their original cores and data, their statement has a more than 75% probability of being true (Fig. 1).

As careful as Hartesveldt et al. (1975) may have been in stating that the General Sherman tree was less than 2500 years old, the National Park Service, perhaps unable to bear such a precipitous decline in the tree's age, instead adopted 2500 years as the midpoint for a range encompassing the tree's estimated age. At the time of this writing, Park literature and the plaque at the General Sherman tree stated that the tree's estimated age was "2300–2700 years." Additionally, a popular book authored by Hartesveldt's colleagues (Harvey et al. 1981) dropped the qualifier "less than," stating instead that the tree ". . . is about 2,500 years old" (though a table on the same page gives the General Sherman tree's age as "2,500–3,000" years!). The most recent estimate of the General Sherman tree's age—2150 years (Fig. 1)—is most closely aligned with Hartesveldt et al.'s (1975) original statement that the tree is less than 2500 years old.

The relative youth of other famous S. giganteum may come as a disappointment to some. For example, the decline in the estimated age of the Grizzly Giant tree has been even more precipitous than that of the General Sherman tree. Clark (1910) reported that the Grizzly Giant had been growing so slowly over the last few centuries that its rings (presumably observed inside of a fire scar cavity) were "as thin as wrapping paper, too fine to be counted with the unaided eye." (On the contrary, measured ring widths [Table 3] and measured tree volume changes [W. Flint personal communication] both indicate that the tree has been growing quite rapidly.) Comparing these purported ring widths with those of some fallen S. giganteum, Clark concluded that

"the Grizzly Giant must be not less than six thousand years old," and that the tree was probably the oldest living thing on earth. Other early age estimates placed the Grizzly Giant at a more modest 3800 years old, while Hartesveldt et al. (1975) later suggested that the tree ". . . is perhaps only 2500 years old." At the time of this writing, the National Park Service reported the age of the Grizzly Giant as 2700 years. However, I estimate the tree to be only about 1790 years old (Fig. 1), and that the probability of it being at least 2700 years old is less than 2%. Hartesveldt and his colleagues (1975) offered solace to those disappointed by the suggestion that certain large S. giganteum might be younger than expected: ". . . this [discovery] effects a change only in superlatives; the world's largest trees are the world's fastest-growing trees."

Some readers may be disappointed by the broad confidence intervals associated with age estimates in Figure 1. There is a great deal of uncertainty in estimating the ages of individual large S. giganteum, largely due to relatively abrupt and sustained changes in ring widths in the part of the bole not sampled by increment cores, and therefore invisible to us (Stephenson and Demetry 1995). Such changes in growth rates are due to unpredictable, site-specific events in the past, such as occasional, localized high-intensity fires (e.g., Mutch and Swetnam 1995). Thus, though Figure 1 suggests that the General Sherman and Sentinel trees are the same age (2150 years), the broad confidence intervals additionally suggest that this correspondence is most likely a meaningless coincidence. However, most of the confidence intervals in Figure 1 are based on relatively short cores. Confidence intervals could be tightened somewhat in the future by taking longer cores and, in the case of the Washington and Cleveland trees, more cores.

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REVIEW

A natural history of the Sonoran Desert. Edited by S. J. Phillips and P. W. Comus. 2000. Arizona-Sonora Desert Museum Press, Tucson AZ, and University of California Press, Berkeley CA. 628 pp. Cloth $55.00 ISBN 0-520-22029-3 Paper $24.00 ISBN 0-520-21980-5.

The staff and associates of the Arizona-Sonora Desert Museum wrote this book as a compilation of their training courses, research, and personal experiences in the Sonoran Desert of Arizona, California, and Mexico. It evolved from the Museum's docent handbook, developed over 30 years as a training document for volunteer interpreters. It provides a summary of numerous biotic and abiotic patterns and processes, emphasizing adaptations of desert organisms and the interrelationships between nature and humans, both past and present. It answers in nontechnical prose typical questions of visitors to the Sonoran Desert. As such, this book covers a wide range of topics within its 628 pages.

The book begins by briefly describing what a desert is, and how the Sonoran Desert differs from other deserts of North America. The regional subdivisions and biomes are nicely summarized based on the original work of Forrest Shreve. The book then launches into two chapters describing a calendar of natural events and ten nature watching hotspots. Although these two chapters are informative and will undoubtedly be of great use to those planning trips to this region, they would make more sense if read after the other chapters and should have been placed at the end of the book, possibly as appendices.

A chapter on desert storms gets the book gets back on track. This is a key chapter appropriately placed near the beginning of the text. It introduces rainfall as a significant factor influencing the evolution of desert organisms and the limitations to human settlement in the Sonoran Desert. Most other chapters that follow presuppose some information contained in this chapter.

The next chapter on desert air and light breaks with the main theme of the book by presenting explanations couched in basic physics. Phenomena such as mirages, atmospheric shimmer, and dust devils are described using simple descriptions of light refraction and the influence of temperature on the behavior of air. Although it is not directly related to the other chapters, it presents an entertaining, effective, and succinct summary and does not significantly detract from the flow of the book.

Consecutive chapters on deep history, geologic origins, soils, human ecology, and biodiversity frame the current Sonoran Desert in the perspective of evolutionary and recent time scales, and set the stage for the meat of the book which is the ecology of plants and animals. The deep history chapter describes changes in flora and fauna over geologic time and discusses relationships between their past and current distributions. The geologic origins chapter describes the geomorphological development of major geologic features. The soils chapter describes the development and physical and biological properties of soils, and their implications for plants and animals. The human ecology chapter describes the influence of humans over the past 12,000 years, ranging from native American hunting, gathering, and farming, to Anglo-American agriculture, mining, and dam building. The chapter on biodiversity defines different indices and scales of biological diversity, describes natural centers of diversity, and explains how humans have reduced diversity by introducing invasive species and converting native plant communities to monoculture farms.

Plants are discussed in separate treatments of plant ecology, flowering plants and grasses. The chapter on plant ecology covers a wide range of topics in its brief 23 pages. Topics include rudimentary descriptions of flower anatomy and photosynthesis, and more detailed descriptions of drought adaptations, pollination, seed dispersal, and flowering seasons. The chapter on flowering plants includes a sampling of the most common and interesting angiosperms (other than grasses) in the Sonoran Desert. It is organized by taxonomic family, within which a few representative species are presented, covering their description, range, and comments on ethnobotany and natural history. The chapter on grasses includes a relatively detailed account of different grassland types and dominant species, including a few dominant aliens, and some original natural history accounts.

Animals are presented in separate sections covering invertebrates, birds, mammals, fishes, reptiles, and amphibians. Adaptations to life in the desert by these groups are summarized. Species accounts of the common or otherwise interesting taxa include descriptions of distinguishing characteristics, habitat, range, life history, and in some cases feeding behavior.

The glossary is very brief, but only includes terms which are not referenced in the extensive index which lists a wide variety of items including common and scientific names, geographic places, and descriptive terms.

This book provides a comprehensive introduction to the natural history of the Sonoran and Mojave deserts, because many examples presented and

species discussed are common to these two deserts. It would be an ideal text for a community college or undergraduate course on desert ecology. Upper division and graduate students would not find much new information in this book. The strength of the book lies in the natural history descriptions for individual species. This information is typically given very short treatment in the floras and field guides of the region, and all readers should find this information interesting and useful.

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California Botanical Society—Meeting Program
2000–2001 Academic Year

All Meetings are held at 7:30 pm in room 2063
in the Valley Life Sciences Building on
the UC Berkeley campus.

September 21, 2000

Predicting the future of Sierran conifer forests: no lessons from the past.
John Battles, Professor, University of California, Berkeley

October 19, 2000

Diversity in California's serpentine plants: the roles of patchiness,
grazing, and burning.
Susan Harrison, Professor, University of California, Davis

November 16, 2000

Restoration of oak woodlands and
grasslands in California: an evolutionary perspective.
Kevin Rice, Professor, University of California, Davis

January 18, 2001

Explosive beauty: rare plant research and management at
Lawrence Livermore National Lab's high explosive test facility, site 300.
Tina Carlsen, Project Leader and Ecologist, Lawrence Livermore National Lab

February 21, 2001

ANNUAL BANQUET and
SEMI-ANNUAL GRADUATE STUDENT MEETINGS
**NOTE CHANGE OF LOCATION: California State University, Chico

The role of geology in molding the California flora
Arthur Kruckeberg, Professor Emeritus, University of Washington

March 15, 2001

Molecular phylogenetic studies in Rosaceae.
Dan Potter, Professor, University of California, Davis

April 19, 2001

Defenders or pretenders? Interactions
between an African acacia tree and four symbiotic ants.
Maureen Stanton, Professor, University of California, Davis

May 17, 2001

Using DNA fingerprinting to study
Sequoia sempervirens populations in Big Basin Redwoods State Park.
Chris Brinegar, Professor, San Jose State University

CONTENTS

⊗ **This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).**

LOCATIONS OF ENDANGERED SPRUCE POPULATIONS IN MÉXICO AND THE DEMOGRAPHY OF *PICEA CHIHUAHUANA*

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Abstract

Picea A. Dietr. (spruce) is an essentially boreal genus, but three endemic taxa occur in México. Coordinates were determined for all known stands to accurately map their range and stimulate their protection, conservation, and study. Thirty-nine stands of *Picea chihuahuana* Martínez (Chihuahua spruce) in the Sierra Madre Occidental were found in three clusters, each separated by 2 to 2.5° of latitude. The southernmost stands occur just south of the Tropic of Cancer. The entire north-south range is 687 km. Mean elevation of southern and central clusters was 2675 m, but stands in the northern cluster averaged over 350 m lower in elevation. *Picea chihuahuana* was associated with steep-sided arroyos or at the base of barrancas (cliffs or gorges).

Picea martinezii T. F. Patterson (Martínez spruce) was found in six stands in the Sierra Madre Oriental, at an elevation of about 2250 to 2650 m and all within 147 km of each other. *Picea mexicana* Martínez (Mexican spruce) occurred on two of the highest ridges in the Sierra Madre Oriental, about 5 km apart and at an elevation of about 3500 m, and on the highest point (3185 m) in Chihuahua in the Sierra Madre Occidental, 676 km to the west. It is probable that *P. mexicana* will be found on one or two other high ridges in the Sierra Madre Oriental.

Every *P. chihuahuana* over 0.3 m in height was counted, measured, and scored for mistletoe infection, fire damage, and crown dieback from unknown cause(s) in 21 stands. Similar observations were made for another 18 stands by Narváez et al. (1983) about 15 years earlier. The combined count was 42,610 *P. chihuahuana*, which includes 24,221 trees and saplings over 2 m tall and 18,389 seedlings under 2 m but over 0.3 m in height. The distribution of diameter classes in our sample of 21 stands was a reverse-J, suggesting that the species is reproducing. However, the ratio of seedlings to saplings and trees was less than 1.0 in all except four of the 39 stands, indicating that the species may actually be in jeopardy.

Based on ring counts from increment cores and stumps, *P. chihuahuana* can reach 272 years of age. This is a relatively short life span compared to other North American spruces. The largest trees were 51 m tall and 125 to 150 cm in diameter-breast-high, and size was about average compared to its congeners in the United States and Canada. Many trees were in poor condition or damaged from cutting, mistletoe, top dieback, and fire.

Contrary to expectations, the southern stands were in no poorer condition than the northern, and in fact, the incidence of mistletoe was highest in the north; this seems to be the first report of mistletoe on *P. chihuahuana*. Trees in southern stands were larger and older, and the ratio of seedlings to saplings and trees was highest in the southern and central stands and lowest in the north.

Resúmen

Los abetos (*Picea* A. Dietr.) son un género esencialmente boreal. A pesar de lo anterior, tres taxa endémicos ocurren en México. Las coordenadas geográficas fueron determinadas para todos los rodales conocidos con el propósito de ubicar de una manera precisa su área de distribución en un mapa y promover su protección, conservación y estudio. Treinta y nueve rodales de *Picea chihuahuana* localizados en la Sierra Madre Occidental estuvieron agrupados en tres clusters, cada uno separado por 2 a 2.5° de latitud. Los rodales más sureños ocurrieron justamente al sur del Trópico de Cáncer. El área entera de distribución de norte a sur fue de 687 km. El promedio de elevación de los clusters del sur al centro fue de 2675 m, sin embargo, en los rodales pertenecientes a los clusters del norte, estos promediaron 350 m más bajos en elevación. *Picea chihuahuana* estuvo asociada con arroyos en pendientes pronunciadas y barrancas.

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Picea martinezii fue encontrada en seis rodales en la Sierra Madre Oriental, a una elevación de cerca de 2250 m a 2650 m y localizados todos a una separación de 147 km uno del otro. *Picea mexicana* ocurrió en dos de los puntos más altos en la Sierra Madre Oriental separados 5 km uno del otro a una elevación cerca de 3500 m, y sobre uno de los puntos más altos (3185 m) en Chihuahua en la Sierra Madre Occidental, 676 km al oeste. Es posible que *Picea mexicana* pudiera ser encontrada sobre uno u otros dos de los puntos mas elevados en la Sierra Madre Oriental.

Cada una de las plántulas de *Picea chihuahuana* arriba de 0.3 m de altura fue contada, medida, y registrada por presencia de infestación de muérdago, daño por incendio, y muerte por despunte de la copa debido a causas desconocidas en 21 rodales. Observaciones similares fueron hechas para otros 18 rodales por Narvaéz et al. (1983) con 15 años de anterioridad. La contabilización combinada fue de 42 610 plantas de *Picea chihuahuana*, la cual incluyó 24 221 árboles adultos y jóvenes fustales arriba de 2 m de alto y 18 389 plántulas abajo de 2 m. La distribución de clases de diámetro en nuestra muestra de 21 rodales tuvo una distribución de una jota invertida, sugiriendo que la especie se esta reproduciendo. Sin embargo, la proporción de plántulas a jóvenes fustales y arboles adultos fue menos de 1.0 en tados, excepto en cuatro de los 39 rodales, indicando que la especie podría realmente estar en peligro de extinción.

Sobre la base del conteó de los anillos de crecimiento en virutas de madera y tocones, *Picea chihuahuana* puede alcanzar hasta 272 años de edad. Esto es un ciclo de vida corto comparado con otras piceas norteamericanas. Los árboles más grandes tuvieron 51 m de alto y de 125 cm a 150 cm de diámetro a la altura del pecho y su tamaño estuvo cerca del promedio comparado con sus congéneres en los Estados Unidos y Canadá. Muchos árboles presentaron una condición pobre o estuvieron dañados por corta, muérdago, despunte de copa por causas indeterminadas, y fuego.

Los datos pueden ser utilizados para monitorar la especie para cambios futuros. La evidencia de fósiles indica que el árca de distribución de *Picea chihuahuana* estuvo confinada hacia el norte durante el Holoceno, y nosotros especulamos que los rodales localizados más hacia el sur podrían estar en una condición mas pobre que aquellos localizados hacia el norte. Contrario a las expectativas, los rodales localizados hacia el sur no estuvieron en una condición muy pobre comparados con aquellos localizados hacia el norte, y de hecho, la incidencia de infestación por muérdago fue más alta en el norte. Los arboles en los rodales del sur fueron más grandes y viejos, y la proporción de plántulas a jóvenes fustales y árboles adultos fue más alta en los rodales del sur y del centro, y más baja en el norte.

The occurrence of *Picea* A. Dietr. (spruce) in the subtropical latitudes of México is surprising. Spruce is a largely boreal genus which, depending on the taxonomist, includes 31 to 50 species (Dallimore and Jackson 1923; Wright 1955; Bobrov 1970; Everett 1981). Three species of spruce occur in cool, temperate, montane forests of México. In the Sierra Madre Occidental, spruce forest occurs less than 38 km from the Río Urique at the bottom of the Barranca del Cobre (the Copper Canyon), where bananas and citrus are grown. Palynological evidence suggests that the spruces of México are relicts stranded by a warming climate during the current interglacial. They may serve the same function as canaries in a coal mine; i.e., by monitoring Mexican spruce populations, we may have an early signal of climate change projected for the next century (Mahlman 1997). The disappearance of cool temperate conifer forest in México is projected under three climate change scenarios (Villers and Trejo 1997).

The most common spruce in México is *Picea chihuahuana* Martínez (Chihuahua or prickly spruce), which occurs in the Sierra Madre Occidental, México's western cordillera (Fig. 1). *Picea chihuahuana* was first reported in 1942 from a site called Talayotes in the State of Chihuahua (Martínez 1953). Locally, it is called cahuite, cahuite espinoso, cahuite bravo, and pinabete espinoso, or, by the native Tarahumara Indians of the Barranca del Cobre, matego or mategoco. Vegetation, soils, and climate at sites where it occurs have been described by Gordon (1968), Narvaéz, Sánchez, and Olivas (1983), and Narvaéz (1984).

Picea mexicana Martínez (Mexican spruce) was discovered in 1961 (Martínez 1961) on Sierra La Marta at the border between the States of Nuevo León and Coahuila (Fig. 1). Cerro El Morro on Sierra La Marta is the highest point (ca. 3700 m) in the Sierra Madre Oriental, the range that parallels the east coast of México. A year earlier, spruce had been reported on Cerro Mohinora (Correll 1960), the highest point in Chihuahua (ca. 3300 m), and these were referred to as *P.* "hybrida" or *P.* "indeterminada". This spruce was very different from *P. chihuahuana* but similar to *P. engelmannii* Engelm. (Engelmann spruce) that reaches its southern limit in the Chiricahua Mountains of southern Arizona about 700 km distant (Little 1971). Using morphological data and multivariate techniques, Taylor and Patterson (1980) found that the trees from Cerro Mohinora clustered with *P. mexicana*. Subsequently, *P. mexicana* and *P.* "indeterminada" were treated as a variety of *P. engelmannii* by Taylor, Patterson, and Harrod (1994); i.e., *P. engelmannii* Parry var. *mexicana* (Martínez) Silba.

In 1983 two stands of spruce, which Müller-Using and Alanís (1984) identified as *P. chihuahuana*, were discovered in the Sierra Madre Oriental in the State of Nuevo León (Fig. 1). However, the nearest populations of *P. chihuahuana* were at least 510 km distant in the Sierra Madre Occidental, separated from the Sierra Madre Oriental by the arid Meseta Central of México. Subsequently, Patterson
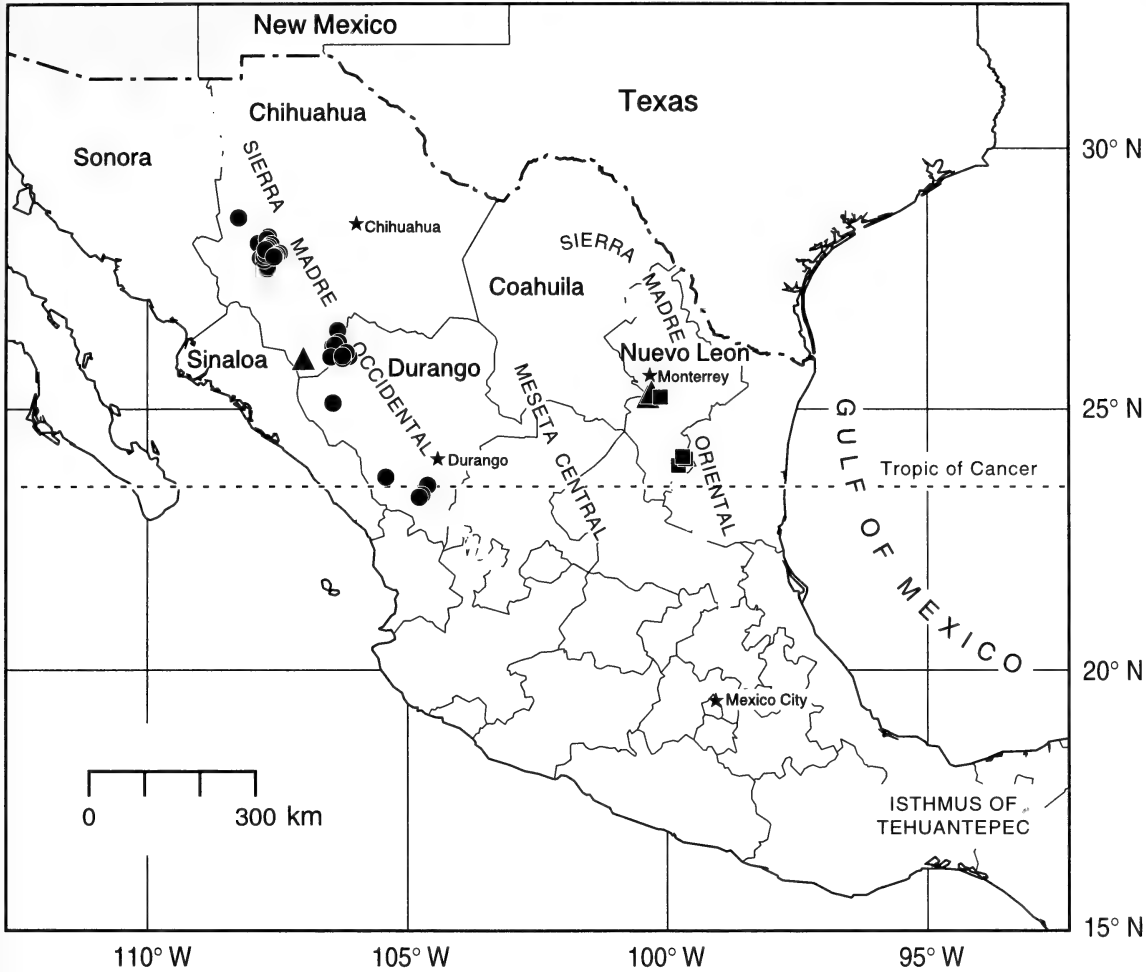
FIG. 1. Map of México showing the locations of Chihuahua spruce (●), Martínez spruce (■), Mexican spruce (▲), and some geographic features mentioned in the text.

(1988) decided that these trees were sufficiently different from *P. chihuahuana* to merit species status, and named them *P. martinezii* T. F. Patterson (Martínez spruce). Needles of *P. martinezii* are flat and flexible and its cone scales have denticulate margins, but the needles of *P. chihuahuana* are four-sided and stiff and its cone scales are rounded. The cones and seeds of *P. martinezii* are larger than those of *P. chihuahuana*. The ecology of *P. martinezii* and *P. mexicana* in the State of Nuevo León was described by Capó et al. (1997).

The endemic spruces are a minor element in the flora of México, yet potentially important from the standpoint of science, their unique contribution to the biodiversity of México, and their value as genetic resources. *Picea chihuahuana* and *P. mexicana* were included on a list of endangered arboreal taxa prepared for the Instituto Nacional de Investigaciónes Forestales y Agropecuarias (INIFAP) by Vera (1990), and all three species qualify as threatened under the guidelines of the International

Union for the Conservation of Nature and Natural Resources (Sánchez 1984; Sánchez and Narvaéz 1990).

Picea chihuahuana occupies sites with some of the richest arboreal species diversities in the Sierra Madre Occidental (Gordon 1968), or in all of temperate North America, and for that reason its habitat should be a crucial focus for protection. The Sierra Madre Occidental was nominated by the IUCN as a global center of plant diversity (Anonymous 1991).

Spruce in México may have retreated northward several times, most recently during Holocene warming. Spruce occurred at least as far south as the Isthmus of Tehuantepec (18°09′N) in the mid-Pliocene, 5 million years ago (Graham 1993). Pollen in the ancient bed of Lake Texcoco, under México City, and in Lake Chalco in the basin of México, show that spruce occurred in the surrounding uplands at the end of the Pleistocene (Clisby and Sears 1955) and at least as recently as 7000 to 8000

yr before present (B.P.; Lozano-García et al. 1993; M.d.S. Lozano-García, personal communication 1997). The nearest *P. chihuahuana* are now about 700 km northwest of México City in the Sierra Madre Occidental, and *P. martinezii* occurs about 500 km north in the Sierra Madre Oriental (Patterson 1988). All *P. mexicana* may have had ranges as far south as México City, but *P. chihuahuana* is most likely to have occurred there. The topography of México is more conducive to migration of high elevation taxa between México City and the Sierra Madre Occidental than between México City and the Sierra Madre Oriental, where *P. martinezii* occurs. In addition, the high endemism of the subalpine habitats in the Sierra Madre Oriental suggests that they were not linked during the Pleistocene with the Transverse Volcanic Belt in which México City lies (McDonald 1993). In any case, palynological and genetic studies indicate that the range of spruce retreated northward since the Pleistocene and all Mexican spruces are now characterized by small, fragmented populations (Ledig et al. 1997).

The southernmost stands of *P. chihuahuana,* Arroyo de la Pista and Arroyo del Chino, lie a few kilometers south of the Tropic of Cancer (23°30′N). Only *P. morrisonicola* Hayata (Morrison spruce) of Taiwan grows at such southerly latitudes (Wright 1955).

No comprehensive description exists to document the location of the Mexican spruces. Previously published information is incomplete, inconsistent, and, in some cases, incorrect. Confusion exists in the spelling of place names, which appear in several variants. Coordinates are sometimes wrong. Many important publications on spruce in México are agency reports or proceedings and not easily obtainable.

A census provides data important to conservation and a baseline against which to monitor the effects of climate change. The increase in temperature at the end of the last glacial was about equal to that projected after a doubling of atmospheric carbon dioxide, which may occur in less than half a century (Mahlman 1997). Spruce was so sensitive to the post-glacial warming that it was reduced from a widespread taxon or group of taxa that occurred as far south as Lake Texcoco to isolated relicts in the highest mountain ranges (Ledig et al. 1997).

An excellent start was made on censusing *P. chihuahuana* by Narváez et al. (1983), and on *P. martinezii* by Müller-Using and Alanís (1984). In Chihuahua, Narváez et al. (1983) counted every *P. chihuahuana* then known, but a census had never been undertaken for Durango, where the southernmost stands occur, and where the continued existence of *P. chihuahuana* may be most in jeopardy because of climatic warming.

Our objective was to accurately map the location of all stands of spruce in México, to make them more accessible for scientific study, and to identify sites worthy of conservation. We anticipate that more stands will be found in time, because botanists have not yet completely explored the rugged mountains of México. Nevertheless, the present inventory is a beginning, and will probably stimulate additional exploration. Our second goal was to complete the census of *P. chihuahuana* begun by Narváez et al. (1983) to provide a baseline against which to measure future change, and to characterize the health of the stands as an aid in making management decisions.

METHODS

Each known location of spruce in México was visited in 1997 or 1998 and its coordinates (latitude, longitude, and elevation) were determined with a geographic positioning system (GPS, Trimble's GeoExplorer). No base stations were available in México, so the data were not corrected for satellite signal degrade introduced by the U.S. Department of Defense through selective availability. However, even with selective availability, the coordinates should not be off more than 100 m and are probably within 50 m of the actual center of the stand. Elevation may vary substantially within stands, and in most cases we took readings at the center and the extremes. Observations were also made of exposure, slope, and land use.

Distance between stands was calculated with an online program (Kindred 1997) and used to group them into geographically coherent clusters using Statistica's clustering module (StatSoft 1995a).

Municipio and land ownership (usually an ejido) were determined in the field. Municipios are divisions of states, roughly equivalent in size and position in the political hierarchy to counties in the United States. Ejidos occur within municipios and are lands given to groups of peasants after the 1910 revolution (Vargas 1996). Ejido lands are often held and used communally. However, parcels may be owned individually if members of the ejido decide that this is appropriate.

By reference to GPS coordinates and topographic features, stand locations were plotted on 1:50,000 maps variously published by: the Comisión de Estudios del Territorio Nacional (CETENAL), Secretaría de la Presidencia; the Departamento Cartografico, Secretaría de la Defensa Nacional; the Instituto Nacional de Estadística, Geografía e Informatica (INEGI); or the Coordinación General de los Servicios Nacionales de Estadística, Geografía e Informatica. Duplicate maps are in the files of the Institute of Forest Genetics, Placerville, CA, and the Centro de Genética Forestal, Chapingo, México.

We counted every *P. chihuahuana* in the State of Durango greater than or equal to 0.3 m tall. During the census, the spruces were marked with paint to ensure that none was counted twice and none overlooked. The stands in Durango were censused during April and May, 1997, except for Arroyo del Chino and Arroyo del Agua, which were only dis-

covered in 1997, and were censused in August and September 1998. In 1998, we also counted spruces at La Luisiana, Arroyo de las Ranas, La "Y", Las Lajas, and Llano Grande in the State of Chihuahua. In June 1999, we counted spruce at Arroyo de Quebrada near El Vergel, Chihuahua. Narvaéz (1984; Narvaéz et al. 1983) censused every stand in Chihuahua known in 1983, but La Luisiana, Arroyo de las Ranas, La "Y", and Las Lajas were not known until 1997, and he omitted Arroyo de Quebrada because he believed that it was in Durango. Our census of Llano Grande unintentionally provided a comparison with Narvaéz' (1984) counts.

In each of the 21 stands censused, we measured height of all spruces ≤3 m but ≥0.3 m tall with a measuring pole, and estimated height of the rest. Diameter-breast-high (dbh at 1.4 m) of spruce over 2 m tall was measured with a graduated scale, called a Biltmore stick. In most stands, more accurate measurements were made on 1000 m² plots in the stand interior. The number of plots in a stand varied from three to 13 to provide a sample equal to approximately 10% of the number of trees ≥10 cm dbh. On the plots, we measured dbh to the nearest millimeter with a diameter tape and height to the nearest meter with a Haga altimeter. In a few stands, plotless samples were measured, and in stands with 15 or fewer trees, we measured every tree with diameter tape and altimeter.

We aged one or two of the large trees in a stand using increment cores taken from standing trees. The very largest trees inevitably had a rotten heart, and it was not possible to age them. We supplemented the increment cores by opportunistically counting rings on stumps. Although *P. chihuahuana* are nominally protected, stumps were observed in many stands. In all, 29 trees were cored, and ring counts were made on 40 stumps.

Finally, we scored condition of the *P. chihuahuana*. We recorded the number with mistletoe, and visually scored the severity of infection on a scale from one to three: 1) one-third of the crown infected, 2) two-thirds of the crown infected, 3) all of the crown infected. Many spruce had dead tops of unknown cause, and we classified these into three categories: 1) one-third of the crown dead, 2) two-thirds of the crown dead, 3) nearly 100% of the crown dead. To summarize these observations, we constructed weighted scores for mistletoe and for crown dieback: the score was the number of spruce in each class multiplied by the severity rating (1 to 3), divided by the total number of spruce. We also presented the data as the percentage of spruce infected with mistletoe or with crown dieback, regardless of severity. If the tree was fire-scarred, that was also recorded.

In reporting the census data, we excluded dead spruce. For regressions of log(height) on log(dbh) and in calculating the means of height and dbh for the interior sample, we excluded dead trees, burned trees, trees with 100% of their crown dead, trees with missing tops, and trees of sprout origin.

Statistical analyses, including regressions, analyses of variance, and post-hoc comparisons of means, were made with Statistica modules for correlation matrices, breakdown and one-way ANOVA, and tables and banners (StatSoft 1995b). However, most of the data presented here for *P. chihuahuana* represent the entire metapopulation, not samples, so significance testing is not actually necessary. All differences are real. Where we present the results of significance tests, it is only to suggest the level of confidence had these stands been a random sample.

RESULTS

Thirty-nine stands of *P. chihuahuana* were located, six of *P. martinezii*, and three of *P. mexicana*. We could not locate the stand of 15 *P. chihuahuana* trees listed in Narvaéz (1984) and Sánchez and Narvaéz (1990) as Río Verde, Ejido Catedral. Martínez (1953) noted *P. chihuahuana* at Arroyos de Urichique, Cuervo, and Meguachic, but we are not certain where he meant. The location of all stands of spruce in México that were known and confirmed as of June 1999 are presented in Tables 1–4 and Fig. 1. Synonyms for place names previously published are listed in the footnotes to Tables 1–4.

Picea chihuahuana occurs between 23°20′N (south of the Tropic of Cancer) and 28°39′N. The distance between the northernmost and the southernmost stand is 687 km. The stands are grouped in three major areas with large gaps between, although Arroyo de Chachamori and Faldeo de Cebollitas are sufficiently isolated that they might be considered their own unique "clusters" (Fig. 1). The largest, northern cluster consists of almost all the stands in Chihuahua immediately north of the Barranca del Cobre, from Arroyo de Chachamori south to Río Vinihueachi. The southern cluster consists of four stands in Durango: Arroyo de la Pista, Arroyo del Chino, Arroyo de las Lagunas, and Arroyo del Infierno. The central cluster is largely in Durango with the exception of one stand, Arroyo de Quebrada, which is in Chihuahua near its border with Durango.

For the 21 stands in Durango and Chihuahua at which we recorded site conditions, all were rocky, 16 abundantly so. In every case, the slope aspect was north to northeast, in only two cases varying as much as 20° west of north. The slope averaged 65%, and was less than 50% only at La Estancia Agua-Amarilla and Arroyo del Infierno, where some of the trees grew on level ground. The spruce generally occurred near the bottoms of canyons or barrancas, sometimes extending nearly to the ridge. Grazing animals were present in all stands except Arroyo de la Pista, Piedra Rayada, Arroyo del Chino, and La 'Y'. Stumps were observed in some

TABLE 1. LOCATION OF CHILHUAHUA SPRUCE STANDS IN THE STATE OF DURANGO, MEXICO. [1] A municipio is a political division of a state. [2] Number and key of the 1:50,000 national topographic maps variously published by the Comisión de Estudios del Territorio Nacional (CETENAL), Secretaría de la Presidencia or the Departamento Cartografico, Secretaría de la Defensa Nacional of the Estados Unidos Mexicanos. [3] In degrees, minutes, and seconds. [4] Elevation recorded by GPS at the center of the stand and rounded to the nearest 5 meters. [5] Synonyms: Arroyo Santa Bárbara (Gordon 1968); Arroyo Santa Bárbara (Taylor and Patterson 1980); Arroyos de Santa Bárbara y Hornitos (Martínez 1953). [6] Ejidos are lands given to groups of peasants after the 1910 revolution and usually held communally. [7] Synonym: Cebollitas (Ledig et al. 1997). [8] Synonym: Arroyo de la Quebrada (Ledig et al. 1997).

Stand	Property	Municipio[1]	Map[2]	Latitude[3] N	Longitude[3] W	Elev.[4] (m)
Arroyo de la Pista	Communidad Santa María Magdalena de Taxicaringa	Mezquital	Guacamayita F13B31	23°19'52"	104°45'00"	2685
Arroyo del Chino	Communidad Santa María Magdalena de Taxicaringa	Mezquital	Guacamayita F13B31	23°21'05"	104°43'05"	2600
Arroyo de las Lagunas	Private Property: Bajíos de Don Victor	Durango	Agua Zarca F13B22	23°31'24"	104°37'20"	2775
Arroyo del Infierno[5]	Ejido[6] El Brillante	Pueblo Nuevo	Pino Gordo F13A28	23°29'40"	105°26'08"	2725
Faldeo de Cebollitas[7]	Private Property: Cebollitas	Canelas	Topia G13C45	25°05'45"	106°26'35"	2450
Arroyo de los Angeles	Ejido El Palomo	Guanaceví	La Medalla G13A86	26°00'17"	106°18'14"	2990
La Estancia-Agua Amarilla	Ejido El Padre y Anexos	Guanaceví	Talayotes G13A85	26°00'41"	106°27'13"	2580
La Medalla	Ejido Llano Grande	Guanaceví	La Medalla G13A86	26°01'56"	106°12'00"	2645
Arroyo del Agua	Ejido El Cedro	Guanaceví	La Medalla G13A86	26°02'49"	106°18'11"	2750
La Medallita	Ejido Llano Grande	Guanaceví	La Medalla G13A86	26°03'14"	106°13'51"	2400
El Saltito	Ejido Llano Grande	Guanaceví	La Medalla G13A86	26°03'40"	106°14'32"	2725
Arroyo de Rosales	Ejido Chiqueros	Guanaceví	Talayotes G13A85	26°11'38"	106°21'54"	2890
Arroyo del Indio Ignacio[8]	Ejido Chiqueros	Guanaceví	Talayotes G13A85	26°08'48"	106°22'53"	2600
Piedra Rayada	Ejido Chiqueros	Guanaceví	Talayotes G13A85	26°09'15"	106°24'17"	2570
Arroyo de Enmedio	Ejido Chiqueros	Guanaceví	Talayotes G13A85	26°11'55"	106°28'13"	2695

stands, most notably Arroyo de los Angeles, Arroyo del Indio Ignacio, and Arroyo del Chino. Saplings were frequently topped for Christmas trees, particularly in Faldeo de Cebollitas, Arroyo de las Ranas, and Arroyo de Quebrada. Damage from fire was noted at Arroyo de la Pista, Arroyo de los Angeles, La Estancia Agua-Amarilla, Arroyo del Agua, Arroyo del Indio Ignacio, Piedra Rayada, Arroyo de Enmedio, and Arroyo de Quebrada. At Arroyo de la Pista the damage to regeneration was severe and at La Estancia Agua-Amarilla a recent fire killed 18% of all stems.

Arboreal associates invariably included *Pinus ayacahuite* var. *brachyptera* Shaw or *P. strobiformis* Engelm., depending on taxonomist (Mexican white pine). Other common associates included *Pinus arizonica* Engelm., *P. durangensis* Martínez, *P. engelmannii* Carrière (yellow pines); *Pseudotsuga* spp. Carrière (Douglas-fir); *Abies durangensis* Martínez (fir); *Juniperus deppeana* Steud., *J. flaccida* Schltdl. (junipers); *Cupressus lusitanica* Mill. var. *benthamii* (Endl.) Carrière (cypress); *Populus tremuloides* Michx (quaking aspen); *Arbutus madrensis* M. S. González-Elizondo (madroño); and *Quercus castanea* Née, *Q. coccolobaefolia* Trelease, *Q. crassifolia* Humboldt et Bonpland, *Q. emoryi* Torrey, *Q. laeta* Liebmann, *Q. oblongifolia* Torrey, *Q. rugosa* Née (oaks). Various shrubs and herbaceous species occurred in the understory (for example, see Gordon 1968).

Picea mexicana spans a latitudinal range from only 25°15′N and 25°58′N, but a wide range of longitude from Cerro Mohinora in the west to Sierra el Coahuilón in the east, a distance of 676 km. The two confirmed stands of *P. mexicana* in Nuevo León are only 5 km apart on opposing ridges separated by the Cañon el Guano. We suspect that *P. mexicana* also occurs on other high ridges in the area. Sierra Potrero de Abrego, a high but relatively inaccessible ridge 9 km to the north of Sierra el Coahuilón, and Sierra la Viga, which is 17 km to the northwest of Sierra el Coahuilón, apparently support alpine-subalpine vegetation (McDonald 1993) and could support *P. mexicana*. Aerial reconnaissance by one of us (C. F.-L.) suggests that spruce occur on Sierra Potrero de Abrego but not on Sierra la Viga.

Picea martinezii is restricted to a range between 23°53′N and 25°11′N, and the two most distant stands are 147 km apart. Additional stands of *P. martinezii* might still be located by aerial reconnaissance.

The elevational range of *P. chihuahuana* is quite narrow. Mean elevation at the center of the stands ranged from about 2155 to 2990 m. Stands occurred at higher elevation in the south than in the north, but there was essentially no difference in elevation between the southern and central clusters (Fig. 2). Elevation of stands in the southern and central clusters averaged 2675 m, with a standard deviation of only 148 m; thus, 95% fall within 2379

to 2971 m, an elevational range of only about 600 m. The mean elevation of stands in the northern cluster was 2317 m with a standard deviation of 93 m; thus, 95% fall within an elevational range of only about 375 m. The elevational range of the northern cluster scarcely overlaps that of the central and southern clusters, and the difference would be significant by Scheffe's test had these been merely samples.

The elevational range for stands of *P. mexicana* was even narrower, about 3350 to 3550 m. *Picea mexicana* is stranded on the absolute highest peaks in both the Sierra Madre Occidental and the Sierra Madre Oriental. The stands of *P. martinezii* were all found in the Sierra Madre Oriental between about 2250 and 2650 m asl.

We divided *P. chihuahuana* into two categories: trees, which were ≥10 cm dbh, and regeneration (seedlings and saplings), which were <10 cm dbh but ≥0.3 m in height. Our census of the 15 known stands of *P. chihuahuana* in Durango and six in Chihuahua totaled 10,943 living trees ≥10 cm dbh and a regeneration of 18,687 (Table 5). In Durango, stands varied from a low of 36 to a high of 6005 spruce (i.e., trees plus regeneration). Several stands in Durango were substantially larger than those in Chihuahua (Table 6), previously censused by Narvaéz (1984).

Apparently, Narváez (1984) used the criterion of 2 m in height to separate his categories of "regeneración" from that of saplings and mature trees ("arbolado joven y adultos"). To make the data sets comparable, we used his criterion, with the result that there were 16,491 trees or saplings over 2 m tall and 13,139 seedlings (or regeneration) in the 15 stands in Durango and the six stands that we counted in Chihuahua (Table 6). Combining our data with that of Narváez (1984), the total number of *P. chihuahuana* is at least 24,221 saplings and mature trees and 18,389 seedlings, or a total count of 42,610 spruce over 0.3 m tall.

We unintentionally included Llano Grande in our census, a stand previously counted by Narvaéz (1984), who mistakenly called it Arroyo Ancho. The duplication provided a comparison between his count and ours. The total number of spruce was very close in the two counts, but the number in individual size classes differed somewhat. Because Narvaéz' (1984) count was made about 15 years earlier than ours, most trees would have grown in the interim, moving from one class (<2 m tall) to the next (>2 m). We tabulated our data into various height categories, and a division at 3 m in height resulted in excellent agreement between Narváez' (1984) count and ours; his 545 saplings and trees versus our 528, and his 370 seedlings versus our 378. Actually, our census also counted 15 dead or burned trees, and if these are added to our tree class, the total is 543, almost the same as Narvaéz' (1984) number of 545. The difference between counts suggests that there has been a slight reduc-

TABLE 2. LOCATION OF CHIHUAHUA SPRUCE STANDS IN THE STATE OF CHIHUAHUA, MEXICO. [1] A municipio is a political division of a state. [2] Number and key of the 1:50,000 national topographic maps of the Estados Unidos Mexicanos, variously published by: the Comisión de Estudios del Territorio Nacional (CETENAL), Secretaría de la Presidencia; the Departamento Cartografico, Secretaría de la Defensa Nacional; the Instituto Nacional de Estadística Geografía e Informatica (INEGI); or the Coordinación General de los Servicios Nacionales de Estadística, Geografía e Informatica. [3] In degrees, minutes, and seconds. [4] Elevation recorded by GPS at the center of the stand and rounded to the nearest 5 meters. [5] Synonym: El Vergel (Martínez 1953). [6] Ejidos are lands given to groups of peasants after the 1910 revolution and usually held communally. [7] Synonyms: Batuybo, spelled here Vatuhibo (Narvaez 1984; Narvaez et al. 1983; Sanchez and Narvaez 1990); possibly Rio Oteros (Taylor and Patterson 1980) and Creel (Taylor et al. 1994). [8] Synonyms: El Pinobetal and San Elias (Narvaez 1984; Narvaez et al. 1983; Sanchez and Narvaez 1990). [9] Occasionally spelled Las Trojes (Narvaez 1984; Narvaez et al. 1983; Sanchez and Narvaez 1990). [10] Synonym: Arroyo de los Talayotes (Martínez 1953). This is the type locality for Chihuahua spruce. [11] Synonyms: Arroyo Situriachic (Taylor and Patterson 1980); Cituriáchic (Martínez 1953). Note that spelling varies for many indigenous place names in this region and the suffixes of "chic" or "chi" are often interchangeable. [12] Synonym: Rancho el Ranchito (Taylor and Patterson 1980). [13] Synonyms: Chachamuri (Naraez 1984; Narvaez et al. 1983; Sanchez and Narvaez 1990); Rio Chachamuri (Sanchez 1984).

Stand	Property	Municipio[1]	Map[2]	Latitude[3] N	Longitude[3] W	Elev.[4] (m)
Arroyo la Quebrada[5]	Ejido[6] El Caldillo y su anexo El Vergel	Balleza	El Vergel G13A75	26°28'12"	106°21'51"	2730
Río Vinihueachi[7]	Private Properties of Vatuhibo and El Venado, and Comunidad San Elías	Bocoyna	San José Guacayvo G13A21	27°44'53"	107°41'58"	2160
El Pinabetal[8]	Comunidad San Elías	Bocoyna	Maguarichic G13A11	27°45'42"	107°41'35"	2305
Las Trojas[9]	Ejido El Ranchito	Bocoyna	Maguarichic G13A11	27°54'27"	107°45'17"	2395
Napahuichi I	Private property La Laja	Bocoyna	San Juanito G13A12	27°54'53"	107°37'10"	2270
Napahuichi II	Private property La Laja	Bocoyna	San Juanito G13A12	27°54'47"	107°37'08"	2340
Talayotes[10]	Ejido Los Volcanes	Bocoyna	Maguarichic G13A11	27°55'03"	107°49'01"	2355
La "Y"	Private property La Laja	Bocoyna	San Juanito G13A12	27°55'23"	107°37'36"	2270
Situriachi[11]	Private property La Laja and Ejido Bocoyna	Bocoyna	San Juanito G13A12	27°55'30"	107°37'49"	2425
Las Águilas	Private property La Laja	Bocoyna	San Juanito G13A12	27°55'35"	107°37'24"	2385
El Realito	Private property La Laja	Bocoyna	San Juanito G13A12	27°55'50"	107°36'43"	2315
El Cuervo	Ejido El Ranchito	Bocoyna	Maguarichic G13A11	27°57'01"	107°46'18"	2475
El Ranchito[12]	Ejido El Ranchito	Bocoyna	Maguarichic G13A11	27°57'20"	107°45'12"	2220
La Tinaja	Ejido El Ranchito	Bocoyna	Maguarichic G13A11	27°57'24"	107°46'08"	2380
Cerro de la Cruz	Ejido San Juanito	Bocoyna	San Juanito G13A12	27°57'44"	107°36'05"	2350

TABLE 2. CONTINUED.

Stand	Property	Municipio[1]	Map[2]	Latitude[3] N	Longitude[3] W	Elev.[4] (m)
Arroyo Ancho	Ejido San Pablo de Sierra	Guerrero	Basigochic H13C81	28°03'58"	107°46'41"	2235
Llano Grande	Ejido Ahuichique	Guerrero	Basigochic H13C81	28°04'40"	107°45'07"	2235
Las Lajas	Ejido Ahuichique	Guerrero	Basigochic H13C81	28°05'51"	107°44'15"	2225
La Luisiana	Private property La Luisiana and Ejido Ahuichique	Guerrero	Basigochic H13C81	28°06'04"	107°42'33"	2360
Mategoina I	Ejido San Pablo de la Sierra	Guerrero	Basigochic H13C81	28°06'18"	107°48'24"	2225
Mategoina II	Ejido San Pablo de la Sierra	Guerrero	Basigochic H13C81	28°06'41"	107°48'41"	2255
Mategoina III	Ejido San Pablo de la Sierra	Guerrero	Basigochic H13C81	28°06'33"	107°48'58"	2155
Arroyo de las Ranas	Ejido Heredia	Guerrero	Basigochic H13C81	28°11'43"	107°41'21"	2530
Arroyo de Chachamori[13]	Ejido Conoachi	Guerrero	Yahuirachic H12D69	28°39'06"	108°16'21"	2320

tion in the number of living trees over the last 15 years.

Stand structure tended to be characterized by a large number of small stems (<5 cm dbh) and progressively decreasing numbers of larger trunks (Fig. 3). However, the ratio of seedlings (<2 m tall) to large spruce was usually less than 1.0 (Table 6). The ratio of seedlings (<2 m tall) to saplings and trees was highest in the south, lower in the central cluster, and lowest in the north: 1.18, 0.72, and 0.53, respectively. The high ratio for the southern cluster was largely due to Arroyo de las Lagunas and if these were samples rather than the entire population, would have missed statistical significance by Scheffe's test (P = 0.052).

The tallest tree of *P. chihuahuana* we measured was 51 m in height at Arroyo de la Pista and the largest diameter was 150 cm at Arroyo de Quebrada. Considering stems ≥10 cm dbh, mean height of sampled trees (i.e., trees in the interior sample plots) varied among stands from 9.8 m at La Luisiana to 25.9 m at Arroyo del Infierno and mean diameter varied from 22.5 cm at Piedra Rayada to 55.6 cm at Arroyo del Infierno (Table 5). In most cases these values were larger than the mean heights and diameters for the entire stand, but are emphasized here because they were taken with greater precision (Haga altimeter and diameter-tape versus ocular estimate and Biltmore stick). Mean height and diameter tended to be greatest in the southern cluster (20.5 m and 42.3 cm), less in the central cluster (16.2 m and 31.7 cm), and least in the four stands that we measured in the northern cluster (12.2 m and 31.7 cm). If these were samples, the differences, between the southern and northern clusters would be statistically significant according to Scheffe's test. Maximum height and diameter (using data for the entire stand) also decreased south to north: mean maximum heights were 45.0, 37.3, and 24.5 m, and mean maximum diameters were 105.9, 98.8, and 59.8 cm, respectively, for the southern, central, and northern clusters. Again, if these were samples, the southern and central clusters would differ significantly from the northern cluster by Scheffe's test.

The logarithms of height and diameter were closely related in all 21 stands in which we took data (Fig. 4). Because the number of observations was so large, tests for homogeneity of regression coefficients (p. 319 in Steel and Torrie 1960) for height on diameter indicated that the slopes differed both between and within clusters. Analysis of variance also showed that the intercepts differed among clusters, and Scheffe's test indicated that the intercepts for the northern cluster were significantly different from those for the central and southern clusters. Although the differences were small, the pattern was consistent; the smallest intercepts (most negative) and largest slopes occurred in the north and the greatest intercepts and smallest slopes in the south (Table 7). For a given diameter, trees were

TABLE 3. LOCATION OF MARTÍNEZ SPRUCE STANDS IN THE STATE OF NUEVO LEÓN, MEXICO. [1] A municipio is a political division of a state. [2] Number and key of the 1:50,000 national topographic maps of the Estados Unidos Mexicanos, published by the Comisión de Estudios del Territorio Nacional (CETENAL), Secretaría de la Presidencia. [3] In degrees, minutes, and seconds. [4] Elevation recorded by GPS at the center of the stand and rounded to the nearest 5 meters. [5] Called La Encantada by Patterson (1988). [6] Ejidos are lands given to groups of peasants after the 1910 revolution and usually held communally. [7] Called El Butano by Paterson (1988).

Stand	Property	Municipio[1]	Map[2]	Latitude[3] N	Longitude[3] W	Elev.[4] (m)
La Tinaja[5]	Ejido[6] La Encantada	Zaragoza	Zaragoza F14A17	23°53'24"	99°47'30"	2515
Agua Fría	Private Property: Agua Fría	Aramberri	Aramberri G14C87	24°02'17"	99°42'39"	1820
Cañada el Puerto I	Private property: Agua de Alardín	Aramberri	Aramberri G14C87	24°02'34"	99°44'04"	2120
Cañada el Puerto II	Private property: Agua de Alardín	Aramberri	Aramberri G14C87	24°02'26"	99°43'54"	2200
Cañada el Puerto III	Private property: Agua de Alardín	Aramberri	Aramberri G14C87	24°02'14"	99°43'55"	2220
Cañón el Butano[7]	Ejido La Trinidad	Montemorelos	Rayones G13C46	25°10'41"	100°07'37"	2180

tallest in the southern cluster and shortest in the northern (e.g., 16.0 m vs. 12.4 m for a tree of 30 cm dbh).

The oldest tree aged from increment cores or from ring counts on stumps was at Arroyo de la Pista and was 272-years-old. All five trees that were aged at Arroyo de la Pista, from stumps or from increment cores, were over 200-years-old.

The condition of many stands was poor due to a combination of factors, including mistletoe, fire, and top dieback of unknown cause(s) (Table 5). Depending on stand, from 0% to 33% of the trees in the 21 stands that we observed were infected with mistletoe; from less than 1% to 46% had fire scars; from 1% to 44% had some degree of top dieback. The percentage of trees infected with mistletoe increased with latitude (r = 0.53), but there seemed to be no geographic pattern with relation to fire or dieback.

DISCUSSION

Thirty-nine stands of *P. chihuahuana* were confirmed. Only 4 sites in Durango and 20 in Chihuahua were known when Narvaéz et al. (1983) published their account. The stands occur in three rather distinct geographic clusters, which we will call the southern, central, and northern clusters. The clusters are about 2 to 2.5° of latitude apart and consist of 4, 12, and 23 stands, respectively. Within clusters, stands are usually within a 20 km radius. However, Arroyo de Chachamori and Faldeo de Cebollitas are somewhat more isolated and could be considered outliers. Although we have been searching for 15 years, we expect that more stands will be found in the future.

Stands are often identified by locals, foresters, and botanists with a variety of names. They may be called by a topographic feature, such as a river or a peak, or by the ejido or property on which they occur. Spelling may vary among sources, because different maps use different variants of the same indigenous word. Situriachic and Situriachi are examples. Furthermore, many names are in common use and confuse the situation. For example, Arroyo de Quebrada is frequently seen on maps, and three stands in Table 2 have been known as Quebrada locally. Llano Grande and Arroyo Ancho, which take their names from ranchos, were reversed by Narvaéz (1984) and Narvaéz et al. (1983). Thus, our Llano Grande corresponds to their Arroyo Ancho.

Use of the GPS coordinates presented here will certainly help in eliminating confusion. Our coordinates can be compared to previously published data for 19 stands (Narvaéz 1984; Narvaéz et al. 1983). Their coordinates seem to be in error for Mategoina I, II, and III, where longitude is about 1° off, a mistake easily introduced when reading coordinates from topographic maps, as Narvaéz et al. (1983) must have done. Previously published

TABLE 4. LOCATION OF MEXICAN SPRUCE STANDS IN THE STATES OF NUEVO LEÓN, COAHUILA, AND CHIHUAHUA, MÉXICO. [1] A municipio is a political division of a state. [2] Number and key of the 1:50,000 national topographic maps of the Estados Unidos Mexicanos, published by the Departamento Cartografíco, Secretaría de la Defensa Nacional or the Instituto Nacional de Estadística Geografía e Informatica (INEGI). [3] In degrees, minutes, and seconds. [4] Recorded by GPS at the center of the stand and rounded to the nearest 5 meters. [5] Synonyms: Sierra de la Martha (Taylor and Patterson 1980; Taylor et al. 1994; but in Nuevo León, not in Coahuila as reported there); El Carmen (Martínez 1961); La Carmen (Rushforth 1986). [6] Ejidos are lands given to groups of peasants after the 1910 revolution and usually held communally.

Stand	Property	Municipio[1]	Map[2]	Latitude[3] N	Longitude[3] W	Elev.[4] (m)
Sierra la Marta[5]	Private Property: Familia Sanchez de la Peña	Rayones, N.L.	San Rafael G14C45	25°11'57"	100°21'48"	3500
Sierra el Coahuilón	Ejido[6] Nuncio	Arteaga, Coah.	San Rafael G14C45	25°14'49"	100°21'12"	3470
El Mohinora	Private Property: El Venadito	Guadalupe y Calvo, Ch.	Mohinora G13C13	25°57'42"	107°02'21"	3185
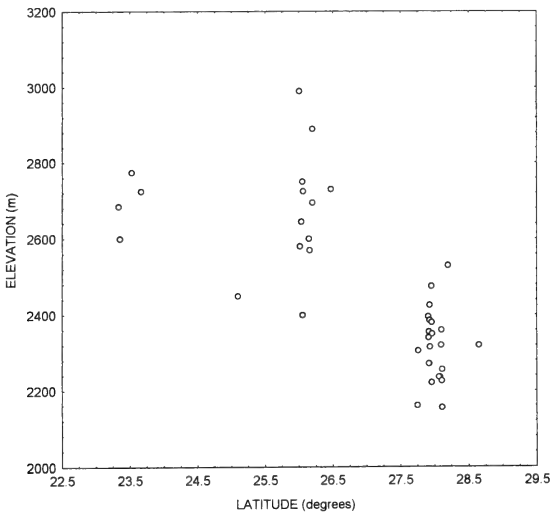
FIG. 2. Scatterplot of elevational coordinates versus latitudinal coordinates for 39 stands of Chihuahua spruce.

coordinates for Arroyo de Chachamori are about 2' in error for latitude and 1.5' for longitude; Narvaéz (1984) and Narvaéz et al. (1983) gave the coordinates for Arroyo de Chachamori in degrees and minutes only, suggesting that they could not locate it with much precision on topographic maps.

For *P. chihuahuana,* stands in the northern cluster were lower in elevation, on average, than those in the central cluster. A species' elevational bounds generally decrease with increasing latitude. In California, species' ranges decrease 172 m in elevation for each increase of a degree in latitude, and in the Rocky Mountains, the change is 77 m (Barbour and Minnich 1999). According to Hopkins' (1938) Law, a change of 1° in latitude is equivalent to 122 m in elevation. Therefore, we expected the central cluster to be 305 m lower in elevation than the southern cluster, however, stands occur at virtually the same elevation in the south and the central clusters. A decrease of 244 m should be expected between the central and northern clusters, but the decrease is actually 352 m. The total decrease in elevation between southern and northern clusters was 379 m, much less than the expected value of 549 m predicted by Hopkins' Law. The explanation may be that *P. chihuahuana* is restricted to sites that attenuate the effects of latitude. More detailed analysis is not possible because climate data are not available for the remote sites where *P. chihuahuana* are found.

Our census is very accurate and we doubt that the counts deviate from actual numbers by more than one percent. Our count at Llano Grande deviates from that of Narvaéz (1984) by less than 1%, despite being separated in time by about 15 years. Fifteen of the trees counted by Narvaéz (1984) now seem to be dead, although still standing. In contrast to the agreement between Narvaéz' (1984) count

TABLE 5. NUMBER OF LIVING TREES ≥10 CM DIAMETER BREAST HIGH (DBH), REGENERATION <10 CM DBH AND ≥0.3 M TALL, MEAN HEIGHT OF SAMPLED TREES, MEAN DBH OF SAMPLED TREES, MEAN DENSITY OF TREES ON SAMPLE PLOTS, AND CONDITION OF ALL 15 STANDS OF CHIHUAHUA SPRUCE IN DURANGO AND 6 IN CHIHUAHUA. [1] Infection by mistletoe, recorded in three severity classes. [2] Dead top from unknown cause(s), recorded in three severity classes. [3] Damaged by fire. [4] The number of affected spruce in each severity class weighted by the class value (1–3) and divided by the total number of trees plus regeneration. [5] The number of spruce affected expressed as a percentage of the total number of spruce ≥0.3 m in height.

Stand	Trees	Regen.	Height (m)	DBH (cm)	Density (ha⁻¹)	Mistletoe[1] Score[4]	%[5]	Top dieback[2] Score[4]	%[5]	Scar[3] (%)
Arroyo de la Pista	599	809	24.7	46.7	63.0	0.001	0.0	0.351	19.5	5.0
Arroyo del Chino	40	10	15.3	36.4	36.6	0.340	26.0	0.500	44.0	46.0
Arroyo de las Lagunas	185	1930	16.1	30.6	97.5	0.00	0.0	0.010	0.9	0.9
Arroyo del Infierno	107	174	25.9	55.6	21.7	0.00	0.0	0.125	6.8	1.4
Faldeo de Cebollitas	83	172	15.5	32.3	22.0	0.00	0.0	0.122	6.3	3.5
Arroyo de los Angeles	1570	4435	16.7	26.0	161.1	0.190	13.3	0.100	7.9	4.5
Estancia-Agua Amarilla	834	855	17.9	32.7	115.7	0.139	11.2	0.377	19.3	11.0
La Medalla	694	1174	16.7	31.8	112.9	0.054	3.4	0.065	4.8	3.5
Arroyo del Agua	375	420	15.5	33.4	78.3	0.486	26.5	0.211	13.8	5.0
La Medallita	264	218	16.0	32.2	62.5	0.224	16.4	0.145	8.5	6.2
El Saltito	472	732	19.9	38.3	84.0	0.151	10.6	0.114	7.1	4.2
Arroyo de Rosales	14	22	19.4	44.0	—	0.361	30.6	0.306	25.0	13.9
Arroyo del Indio Ignacio	1563	2587	13.5	25.5	130.0	0.114	7.9	0.118	8.0	3.2
Piedra Rayada	2342	3204	12.5	22.5	187.7	0.111	8.2	0.097	7.2	4.3
Arroyo de Enmedio	316	832	15.4	27.2	126.7	0.072	3.7	0.083	3.3	0.6
Arroyo de Quebrada	765	475	15.4	34.0	122.9	0.348	25.7	0.379	26.0	17.3
La "Y"	11	10	11.7	27.7	—	0.476	33.3	0.286	28.6	4.8
Llano Grande	480	407	13.5	30.0	—	0.306	21.5	0.268	20.4	14.5
Las Lajas	15	11	10.8	33.5	—	0.462	26.9	0.346	19.2	11.5
La Luisiana	92	90	9.8	28.4	—	0.253	18.7	0.275	22.0	9.9
Arroyo de las Ranas	122	120	15.3	38.8	—	0.182	14.9	0.161	12.4	22.3

and ours, our count of 107 stems ≥10 cm dbh, or even 56 stems ≥30 cm, dbh is in excess of the 36 trees and 9 seedlings recorded at Arroyo del Infierno by Gordon (1968).

Combining our data with that of Narváez (1984), the total number of *P. chihuahuana* ≥2 m in height is a sizeable figure, 24,221, and the number of seedlings <2 m and ≥0.3 m is about 18,389.

Density of *P. chihuahuana* ≥10 cm dbh, derived from the 1000 m² plots located in the centers of the stands, averaged 94.8 ha⁻¹ with a range for 15 stands from 21.7 to 187.7 ha⁻¹ (Table 5). Although the data are not completely comparable, density was slightly lower in the 18 stands reported by Narváez et al. (1983), which had a mean of 72.8 and a range of 25.4 to 117.0 trees >2 m tall ha⁻¹. *Picea chihuahuana* stands are similar to but, perhaps, slightly less dense than stands of *P. breweriana* S. Watson, (Brewer spruce) which may range from about 125 to 320 trees ≥10 cm dbh ha⁻¹ (Thornburgh 1990), or stands of *P. sitchensis* (Bong.) Carriére, (Sitka spruce) which have about 188 trees ha⁻¹ (Harris 1990). However, density of boreal and other north temperate spruces is much higher: 815 to 1324 trees ha⁻¹ for well stocked *P. glauca* (Moench) Voss (white spruce) stands in Alaska and Saskatchewan (Nienstaedt and Zasada 1990); 1110 to 1780 trees ha⁻¹ of *P. mariana* (Mill.) B.S.P. (black spruce) in Ontario (Viereck and Johnston 1990); 140 to 780 *P. engelmannii* ≥4 inches (ap-

proximately 10 cm) dbh in mixed spruce-fir forests in Wyoming (Oosting and Billings 1951); and 121 to 480 trees ha⁻¹ *P. rubens* Sarg. (red spruce) in the Maritime Provinces and Maine (Blum 1990; Oosting and Reed 1942).

Though we have not counted the trees of *P. mexicana*, they are numerous, perhaps in the thousands, at all three confirmed sites. Rushforth (1986) mistakenly reported that the stand at Sierra La Marta was reduced to six trees at the top of the range. A fire in 1975 destroyed the type locality on the lower slopes of Sierra la Marta, and most of the spruces, but many hundreds escaped damage in a cañada (a precipitous cleft smaller than a canyon) high on the mountain.

Müller-Using and Alanís (1984) counted 68 *P. martinezii* ≥10 cm dbh at La Tinaja and 350 at Cañon el Butano. The number at Agua Fría, recently discovered, may exceed the number at Cañon el Butano. Nevertheless, *P. martinezii* is extremely rare.

Our data from increment-cored trees was insufficient to construct precise height-age and dbh-age relationships because of the limited range in age of the trees we bored. However, Gordon (1968) presented relationships based on stem analyses and Narváez (1984) presented scatterplots of height and diameter on age for 37 trees spanning a range from about 20 to 120 yr. Based on Narváez' (1984) scatterplots, spruce on the ten sites he sampled in Chi-

TABLE 6. NUMBERS OF TREES AND SAPLINGS (T ≥ 2 M TALL), SEEDLINGS (S < 2 M TALL), AND THE RATIO SEEDLINGS/ TREES + SAPLINGS FOR ALL 39 CONFIRMED STANDS OF CHIHUAHUA SPRUCE. [1] We did not include seedlings <0.3 m tall; data for Narvaez (1984) apparently does. [2] Counts made in April and May 1997. [3] Counts made in August and September 1998. [4] Count made in June 1999. [5] Counts reported in Narvaez (1984), which differ from counts in Narvaez et al. (1983). [6] During seed collections, we found only 17 trees, most with dead tops, and stumps, indicating that the population has declined in the last 15 years. [7] Called Llano Grande by Narvaez (1984) and Narvaez et al. (1983).

Stand	T	S[1]	Total	S/T
Arroyo de la Pista[2]	919	489	1408	0.532
Arroyo del Chino[3]	46	4	50	0.087
Arroyo de las Lagunas[2]	505	1610	2115	3.188
Arroyo del Infierno[2]	148	133	281	0.899
Faldeo de Cebollitas[2]	172	83	255	0.483
Arroyo de los Angeles[2]	2507	3498	6005	1.395
La Estancia-Agua Amarilla[2]	1195	494	1689	0.413
La Medalla[2]	1012	856	1868	0.846
Arroyo del Agua[2]	510	285	795	0.559
La Medallita[2]	356	126	482	0.354
El Saltito[2]	656	548	1204	0.835
Arroyo de Rosales[2]	21	15	36	0.714
Arroyo del Indio Ignacio[2]	2628	1522	4150	0.579
Piedra Rayada[2]	3564	1982	5546	0.556
Arroyo de Enmedio[2]	465	683	1148	1.469
Arroyo de Quebrada[4]	877	363	1240	0.414
Río Vinihueachi[5]	1785	1579	3364	0.885
El Pinabetal[5]	455	267	722	0.587
Las Trojas[5]	874	780	1654	0.892
Napahuichi I[5]	1064	921	1985	0.866
Napahuichi II[5]	209	150	359	0.718
Talayotes[5]	291	299	590	1.027
La "Y"[3]	13	8	21	0.615
Situriachi[5]	389	286	675	0.735
Las Águilas[5]	548	168	716	0.307
El Realito[5]	587	210	797	0.358
El Cuervo[5]	140	96	236	0.686
El Ranchito[5]	217	162	379	0.747
La Tinaja[5]	99	37	136	0.374
Cerro de la Cruz[5,6]	20	5	25	0.250
Llano Grande[5]	545	370	915	0.679
Llano Grande[3]	614	273	887	0.445
Arroyo Ancho[5,7]	127	8	135	0.063
Las Lajas[3]	19	7	26	0.368
La Luisiana[3]	127	55	182	0.433
Mategoina I[5]	124	29	153	0.234
Mategoina II[5]	448	164	612	0.366
Mategoina III[5]	207	65	272	0.314
Arroyo de las Ranas[3]	137	105	242	0.766
Arroyo de Chachamori[5]	146	24	170	0.164
Total	24,221	18,389	42,610	0.759

huahua would be about 29 m tall at 100 yr of age. Gordon's (1968) stem analyses suggest a height of 28 m at 100 yr on a moist site at Arroyo del Infierno in Durango, but only 12 m for a poorer site. Based on a regression of height on age for the 29 trees we bored (r = 0.49), we would expect a height of about 24 m at age 100. Thus, *P. chihuahuana* probably grows slowly, about one-quarter to one-third of a meter per year, on average, over its first 100 years.

Compared to other North American spruces, *P. chihuahuana* does not seem particularly long-lived. Most of the large *P. chihuahuana* that we cored had between 100 and 200 rings at breast height. How-ever, the largest trees had heart rot, which made it impossible to age them. Sánchez and Narvaéz (1990) reported finding wood rot in 40% of adult trees, possibly caused by fungi belonging to one or more of the genera *Alternaria, Helminthosporum, Nigrospora, Sporotrichum,* or *Trichoderma.* The oldest trees that we bored were 272- and 244-yr-old at breast height, and several stumps had over 200 rings. By contrast to *P. chihuahuana,* the oldest *P. breweriana* might be 900 yr (Waring, Emmingham, and Running 1975); *P. sitchensis* may live to 700 or 800 yr (Harris 1990); trees of *P. engelmannii* between 500 and 600 yr of age are "not uncommon" (Alexander and Shepperd 1990) and can sur-
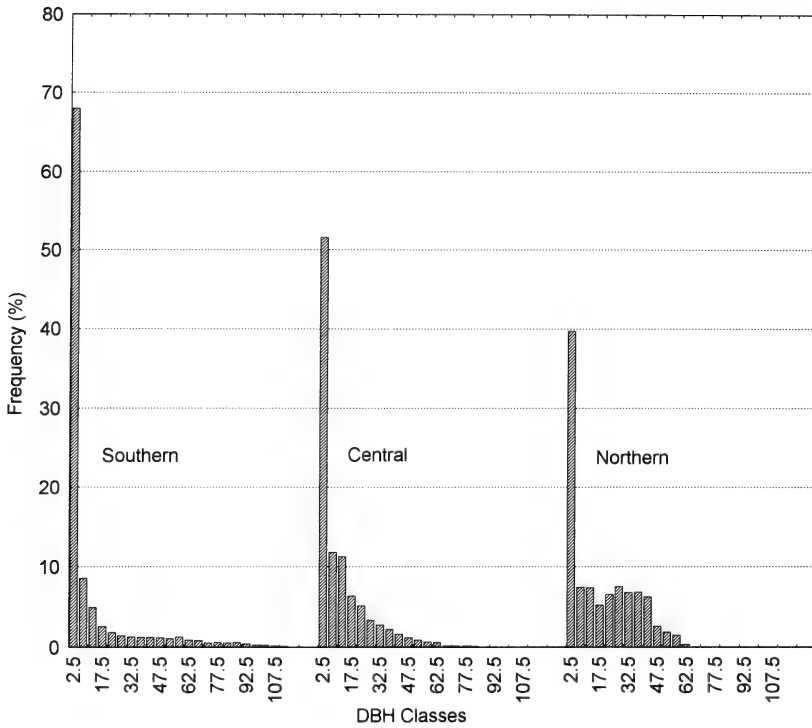
Fig. 3.   Frequency of observations in 5 cm-dbh classes plotted over the class mid-point for all Chihuahua spruce ≥0.3 m tall in the southern, central, and northern clusters of stands.

vive to 680 yr (Brown et al. 1995); *P. pungens* Engelm. (blue spruce) may survive to 600 yr or more (Fechner 1990); and the maximum age in *P. rubens* is about 400 yr (Blum 1990). The oldest *P. glauca* on good sites may be 250 to 300 yr, similar to *P. chihuahuana,* but above the Arctic Circle, slow-growing *P. glauca* may reach 1000 yr (Nienstaedt and Zasada 1990). *Picea mariana,* alone of the North American spruces, may be slightly shorter-lived than *P. chihuahuana,* but *P. mariana* of 280 yr have been reported (Viereck and Johnson 1990). Müller-Using and Lässig (1986) found a *P. martinezii* with a ring count of 279 at breast height.

With regard to ultimate size, *P. chihuahuana* is average among the North American spruces. The largest trees were in the southern cluster and were about 50 m in height and 125 cm dbh. Size seemed to decrease from the southern to the northern cluster. The largest *P. martinezii* were only 32 m tall and 62 cm dbh (Müller-Using and Lässig 1986). The largest *P. breweriana, P. engelmannii,* and *P. pungens* are very close in height and diameter to *P. chihuahuana* (Thornburgh 1990; Waring et al. 1975; Alexander and Shepperd 1990; Fechner 1990). *Picea glauca* may be slightly smaller, the largest being about 55 m by 120 cm (Nienstaedt and Zasada 1990). *Picea mariana* and *P. rubens* are substantially smaller, reaching 27 m height by 46 cm dbh and 35 m height by 61 cm dbh, respectively (Viereck and Johnson 1990; Blum 1990). On the

other extreme, *P. sitchensis* is a giant, the largest being about 66 m by 510 cm (Harris 1990).

Many *P. chihuahuana* were in poor condition or damaged. Within the 21 stands that we studied, from 1% to 44% of the trees had dead tops from unknown causes. The severity varied from a third to almost the complete crown, and incidence tended to be higher in smaller stands (Table 5). Dead tops were also observed by Narvaéz (1984) and Narvaéz et al. (1983), but only in 1.3% of the spruces in the State of Chihuahua. We found that 19% of the spruces had some degree of dieback in the five stands we observed in the northern cluster, including 181 of 887 spruce (20%) at Llano Grande, which was also scored by Narvaéz (1984). Narvaéz (1984) recorded only 4 of 915 spruce with top dieback, "puntisecos". Perhaps, the condition has become substantially worse in the 15 years between observations. Or, perhaps, Narvaéz (1984) scored only the most severely affected trees. In our sample of five stands in Chihuahua, only 2.2% of the trees ≥10 cm dbh had tops with complete dieback, but 33.2% had dieback of less severity.

In any case, damage from top dieback and other causes is extensive, and further threatens this rare species. Fire scars were noted in every stand, and reached high proportions, up to 46% in some smaller stands. In the survey of Sánchez and Narvaéz (1990), only 3.4% of the spruce were damaged by fire. Even though *P. chihuahuana* is nominally pro-
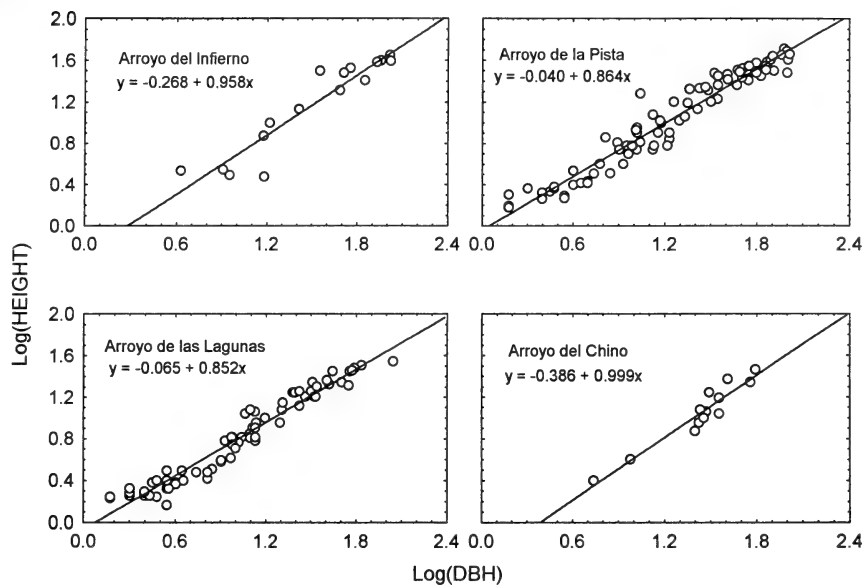
FIG. 4.   Regression of log(height in m) on log(dbh in cm) for a sample of 190 Chihuahua spruces from the southern cluster of stands (Arroyo del Infierno, Arroyo de la Pista, Arroyo de las Lagunas, and Arroyo del Chino).

tected, clandestine cutting occurs, as evidenced by the 40 stumps on which we made ring counts. Many other trees were topped for Christmas decorations.

Our observation of mistletoe seems to be the first report on *P. chihuahuana* (Hawksworth and Wiens 1996), and we have not identified the species. We observed mistletoe on spruce in some stands, but not in all. Mistletoe was least common and the frequency of infected trees was least in the southern cluster and greatest in the northern cluster, where it exceeded 19%. Sánchez and Narvaéz (1990) did not mention mistletoe. Dwarf mistletoes are damaging to all other North American spruces north of México. *Arceuthobium microcarpum* causes heavy mortality to *P. engelmannii* in Arizona and New Mexico, but is not found farther north (Alexander and Shepperd 1990). It also colonizes *P. pungens* (Fechner 1990). In some stands, 36% of *P. breweriana* are parasitized by *A. campylodum* (Thornburgh 1990), which may destroy infected trees. *A. pusillum* is common and destructive on black spruce in eastern North America, but absent in the West (Viereck and Johnston 1990), and it also col-

onizes *P. glauca* (Nienstaedt and Zasada 1990), and, occasionally, *P. rubens* (Blum 1990).

Some stands seemed to be in poorer health than others, and these included some of the smallest stands. For example, the number of spruce at Arroyo del Chino was only 50, and 44% of these had tops affected to various degrees by dieback, 46% were scarred by fire, and 26% had mistletoe. In addition, the ratio of seedlings to trees and saplings was only 0.087. It may be very difficult to conserve such stands, and we suggest that seeds or cuttings be collected as soon as possible to conserve their genetic resources. The most threatened stands can be identified in Tables 5 and 6.

The most critical question with regard to the conservation of *P. chihuahuana* is whether the stands are regenerating adequately. The distribution of spruce into 5 cm diameter-size classes forms a reverse J-shape (Fig. 3) in most stands, particularly the large ones. This suggests that the older trees will be replaced. However, this may be misleading. The ratio of seedlings <2 m tall to trees and saplings ≥2 m is less than 1.0 in all except four of 39 stands for which data exist. One of these, Arroyo

TABLE 7.   REGRESSION COEFFICIENTS (B) AND INTERCEPTS (A) OF LOG(HEIGHT IN M) ON LOG(DBH in cm), with Standard Errors (in Parentheses), and Correlation Coefficients (R) in Chihuahua Spruce from Northern, Central, and Southern Clusters. [1] Five stands are represented in the northern cluster, 12 in the central, and 4 in the southern. [2] Number of trees, from the interior plots in each stand.

Cluster[1]	n^2	b	a	r
northern	341	0.9524 (0.0221)	−0.3145 (0.0306)	0.920
central	1235	0.8704 (0.0097)	−0.0944 (0.0125)	0.938
southern	193	0.8458 (0.0188)	−0.0461 (0.0247)	0.956

de las Lagunas, was heavily logged somewhat over a decade ago, removing many of the large trees, which may explain the high ratio of 3.19 seedlings to saplings and trees. In many stands, the number of trees ≥10 cm dbh exceeds the number of seedlings <2 m tall, suggesting that the stands are in trouble.

We believe that the ratio of seedlings to trees is significant because *P. chihuahuana* probably regenerates in the shade. Although ecological studies of *P. chihuahuana* are lacking on this point, other North American spruces, such as *P. breweriana, P. engelmannii, P. glauca, P. rubens, P. mariana,* and *P. sitchensis* are tolerant of shade. In fact, *P. breweriana* and *P. engelmannii* seedlings cannot survive strong sunlight (Thornburgh 1990; Alexander and Shepperd 1990; Ronco 1975), and regeneration of *P. pungens, P. rubens,* and *P. sitchensis* benefits from shade (Fechner 1990; Blum 1990; Harris 1990). All spruces north of México are thin-barked and highly susceptible to fire, and do not normally require disturbance for regeneration, with the exception of the partially serotinous *P. mariana.*

The ratio of seedlings to saplings and trees in some other North American spruces seems at least twice that observed in *P. chihuahuana.* However, comparison with other studies is difficult because of differences in methodology and presentation of data. In *P. rubens,* the ratio of stems ≤10 ft tall to stems >10 ft was 1.87 for a 60-yr-old stand in Maine (Oosting and Reed 1942). In eight stands of *P. engelmannii* in Wyoming, the ratio of stems ≤8 ft tall to stems >8 ft averaged 2.34, ranging from 0.24 to 7.33 (Oosting and Reed 1952). For seven stands in the Smoky Mountains of North Carolina and Tennessee, the ratio of *P. rubens* stems <2 inches dbh to stems ≥2 inches was 8.45, and in four stands in the White Mountains of New Hampshire, the ratio was 23.81, with a range of 22.26 to 26.85 (Oosting and Billings 1951). A 2-inch diameter limit is roughly equivalent to a 3 m tall *P. chihuahuana* (from Table 7). If Oosting and Billings' (1951) 1-inch diameter limit is used (equivalent to a 1.5 m tall *P. chihuahuana*), the ratios of *P. rubens* regeneration to trees was 5.24 in the Smoky Mountains and 13.34 in the White Mountains.

Global warming is a threat to the cool temperate conifer forest of México (Villers and Trejo 1997). Therefore, we might expect the stands in the southern cluster to be in greater decline than those in the central cluster, and those in the central cluster to be in greater decline than those in the northern cluster. This does not yet seem to be the case. The ratio of seedlings to saplings and trees was 1.18, 0.72, and 0.53 for the southern, central, and northern clusters, respectively. However, trees were larger on average in the south and smallest in the north, suggesting that northern stands are younger and will survive longer without replacement.

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REVISION OF *CORETHROGYNE* (COMPOSITAE: ASTEREAE)

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ABSTRACT

Review of variation in morphological characters within and among natural populations and comparisons of greenhouse-grown plants, coupled with high pollen stainabilities in progeny from crosses of plants from different populations, led to the conclusion that *Corethrogyne* should be treated taxonomically as comprising a single species with two varieties. The revised taxonomy results in the new combination **Corethrogyne filaginifolia** var. **californica.**

Corethrogynes occur, as scattered, local populations, from Coos Co., Oregon, south through much of California into northern Baja California, from sea level along the immediate coast to ca. 2500 m in the Sierra Nevada. Keck (1959) recognized three species of *Corethrogyne* DC.; Ferris (1960) recognized seven species. Lane (1992, 1993) treated the type species of *Corethrogyne* and *Lessingia* Chamisso as congeneric and, based in part on the work summarized here, treated the corethrogynes of Keck and Ferris as two varieties in one species of *Lessingia.*

Morphological variation within and among populations of these plants is considerable and is reflected in the 33 basionyms that have been linked to the generic name *Corethrogyne.* The 30 'taxa' referable here to *Corethrogyne* have been distinguished mainly by traditional morphological characteristics such as habit, size and shape of leaves, number of heads per flowering stem, size of heads, and shape of involucres. Aspects of indument such as relative amounts of tomentum and/or stipitate-glandular hairs have also been used in drawing circumscriptions.

Field observations by Saroyan indicated that plants with characteristics of reputedly allopatric 'taxa' sometimes grow together in local populations. Plants with heads (including rays) 15 vs. 30 mm wide (assignable to two distinct 'species'), plants with leaves 5 vs. 19 mm wide (different 'species'), or plants with involucres 7 vs. 12 mm long (different 'species' or different 'varieties') are found in local populations, represent extremes of continua, and exemplify the kinds of problems that are found in past taxonomies. Such problems of reconciling taxonomy and plants did not go unnoticed by Keck or Ferris.

"This imperfectly known sp. [*C. leucophylla*] recombines the characters of the other two [*C. californica* and *C. filaginifolia* sensu Keck] and needs further study." —Keck (1959).

"Relatively few individual collections in any given range completely conform to the type and the original description. Intermediate forms abound . . .." —Ferris (1960).

On transfer of *Corethrogyne* to *Lessingia,* Lane (1992) emphasized morphological and chemical (chloroplast DNA) similarities. We emphasize the differences, as did Jones (1977), who compared corethrogynes and lessingias and concluded, "It would serve no useful purpose to argue for a congeneric status."

The genera are readily distinguished:
Plants perennial; heads radiate . . . . . *Corethrogyne*
Plants annual; heads discoid or ± radiant (corollas of peripheral florets often strongly zygomorphic) . . . . *Lessingia*

MATERIALS AND METHODS

This paper is based on an unpublished thesis (Saroyan 1974).

In addition to traditional field observations made up and down California and traditional review of specimens in herbaria (ca. 1500 sheets from 17 herbaria - see Acknowledgments), Saroyan (1974) studied morphological variation in samples from 20 populations of *Corethrogyne* from northern to southern California (A–T in Appendix 1). Each population was associated with one of three vegetation types: type I, grasslands; type II, coastal scrub and chaparral; and type III, forest. For each of the study populations, one to five plants grown from seed in greenhouses in Hayward, CA were
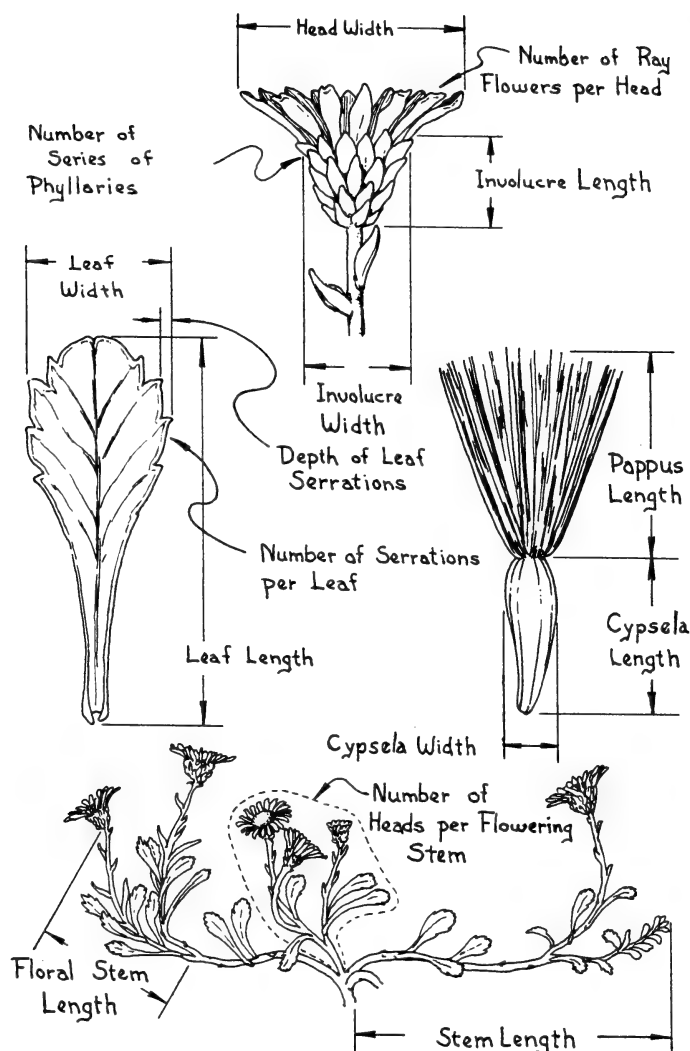
Fig. 1. Characters of a generalized *Corethrogyne*.

used in tests of self-compatibility and in inter-population crosses and served as tests for phenotypic plasticity in the study populations.

Saroyan (1974) chose characters that have been used in taxonomy of Compositae in general and/or in *Corethrogyne* in particular and that could be easily assessed statistically (cf. Fig. 1). He determined mean, standard error of the mean, and range of values for: 1) length of stem, 2) length of leaf, 3) width of leaf, 4) length of floral stem, 5) number of heads per flowering stem, 6) width of head, 7) number of ray florets per head, 8) length of involucre, 9) diameter of involucre, 10) number of series of phyllaries, 11) number of serrations per leaf, 12) depth of leaf serrations, 13) length of cypsela, 14) width of cypsela, 15) length of pappus, 16) ratio length/width of leaf, and 17) ratio length/diameter of involucre.

To determine minimum adequate sample size for representative statistics for morphological characters in wild populations, Saroyan selected samples of 25, 50, and 100 plants from one such population; data from those three samples were pooled to give a fourth sample of 175 plants. Comparisons of F-test statistics for the four samples indicated that reliable results could be achieved from a sample size of 50 individuals. Fifty plants were randomly selected in the field from each of the 20 study populations by use of a grid and a table of random numbers, yielding a grand total of 1000 plants sampled.

Sampling of individual structures was also randomized. For some characters, all like structures (e.g., heads at mid anthesis) were removed from a plant and tossed into a paper bag, then one was extracted blindly for measurement. For other characters, the structure to be measured was chosen by association with a table of random numbers. Mean,

standard error of the mean, and range were determined for each set of 50 measurements.

Chromosome counts were made from microsporocytes fixed in acetic ethanol (3:1, v:v) and stained in aceto-carmine for 2–13 plants from each study population. Pollen was stained in lactophenol-cotton blue for 1–13 plants (300 grains counted for each plant) from each study population.

Vouchers for each study population and representative greenhouse-grown plants (including progeny from crosses made in the greenhouse) were deposited in UC.

RESULTS AND DISCUSSION

Character by character comparisons across the 20 study populations confirmed our impression of general morphological continuity within *Corethrogyne*. Not only ranges of absolute values but even measures of two standard errors of the mean for any one population overlapped with the same values or measures for some or all of the other 19 populations (e.g., length of stem and width of head; cf. Fig. 2). Nevertheless, the five northern populations (A–E in Appendix 1) showed coherence and were somewhat distinct from the southern ones (F–T in Appendix 1) for some characters (e.g., number of heads per flowering stem and the ratio length/diameter of involucre; cf. Fig. 3).

Variation in single characters seldom showed clear correlations with environmental or habitat parameters. Plants from coastal populations usually had shorter, more prostrate stems; plants from inland populations were usually more erect. The four populations with longest and narrowest leaves were the four associated with chaparral or coastal scrub vegetation; they were not distinctive for other characters.

Morphologies of greenhouse-grown progeny from each of the study populations were similar to those of parental plants. Evidently, phenotypic plasticity is not strong for any of the characters examined.

All published reports of chromosome number (see standard indices; e.g., Goldblatt and Johnson 1992) for *Corethrogyne* have given $2n = 10$ (some as $n = 5$; some as $2n = 5$ II). Similarly, we found meiosis to be regular with $2n = 5$ II in all of our samples, including the interpopulational hybrids. Pollen stainabilities in our study populations ranged from 80 to 97 percent (Appendix 1). One or more plants grown from seed collected from each study population were self-pollinated; none set viable seeds. Inter-population crosses of one to five pairs of plants in the combinations E × H, N × H, J × D, and M × C (cf. Appendix 1) yielded hybrids with no obvious irregularities at meiosis and with pollen stainabilities of 82 to 96 percent.

In general aspect, some local populations of *Corethrogyne* are strikingly different from others. Nevertheless, overlap and continuity in expression of most morphological characters, coupled with cross-compatibility between plants from quite disjunct and dissimilar populations, have led us to treat *Corethrogyne* as comprising a single species. Plants from the northwestern part of the range of the species usually have fewer heads on each flowering stem and have larger heads than do plants from other areas; we have recognized them as a variety.

TAXONOMY

CORETHROGYNE DC., Prodr. 5:215. 1836. —Type: *Corethrogyne californica* DC.

Herbaceous or suffrutescent perennials, primary stems decumbent to ascending or erect, mostly 1–10 dm long, usually densely white-tomentose, sometimes becoming glabrate and/or glandular distally. Leaves alternate, often crowded at bases of stems, sessile or with bases of blades ± decurrent on petioles, blades ovate to spatulate, oblanceolate, or linear, 1–7+ cm long, 3–19+ mm wide, becoming smaller, sessile, and bractlike distally, margins entire or variously toothed. Heads pedunculate or sessile, 1–20+ per floral stem. Involucres hemispheric to campanulate, turbinate, or cylindric, 6–14 mm long, 3–10 mm in diam. Phyllaries 30–90+, strongly graduated in 3–9 series, narrowly lanceolate to linear, cartilaginous to scarious with herbaceous, often spreading to squarrose tips, becoming deflexed as cypselae are shed. Ray florets 10–43 in 1 series, neutral, corollas purplish through violet and pink to white, laminae ± linear. Disc florets 12–120+, bisexual, corollas yellow, actinomorphic, 4–8 mm long, tubes 0.6–1.4 mm long, glabrous, throats very narrowly cylindric, 2.8–5.5 mm long, often sparsely puberulent, lobes equal, narrowly lanceolate, 0.7–1.2 mm long, sparsely to densely glandular-puberulent abaxially, papillate-ciliolate on margins and/or adaxially; style branches linear with blunt to subulate appendages, ± hispid with rigid yellow hairs, the appendages to half as long as the stigmatic lines. Cypselae cuneiform to linear, mostly 2–5 mm long, 5–7-ribbed, puberulent to pilose. Pappi of 35–65 coarse, unequal, brownish to reddish bristles 3–8 mm long. Chromosomes: $2n = 10$.

As treated here the genus is monotypic.

CORETHROGYNE FILAGINIFOLIA (Hook. & Arn.) Nutt., Trans. Amer. Phil. Soc., ser. 2. 7:290. 1840 [1841]. ≡ *Aster? filaginifolius* Hook. & Arn., Bot. Beechey voy. 146. 1833. ≡ *Corethrogyne californica* DC. [var.] *filaginifolia* (Hook. & Arn.) Kuntze, Rev. gen. pl. 1:330. 1891 [illegit., oldest sp. epithet not used]. ≡ *Corethrogyne filaginifolia* (Hook. & Arn.) Nutt. var. *typica* M. L. Canby, Bull. S. Calif. Acad. Sci. 26:10. 1927. = *Lessingia filaginifolia* (Hook. & Arn.) M. A. Lane, Novon 2:213. 1992. —Type: California, *F. W. Beechey et al. s.n.* (holotype: E!).
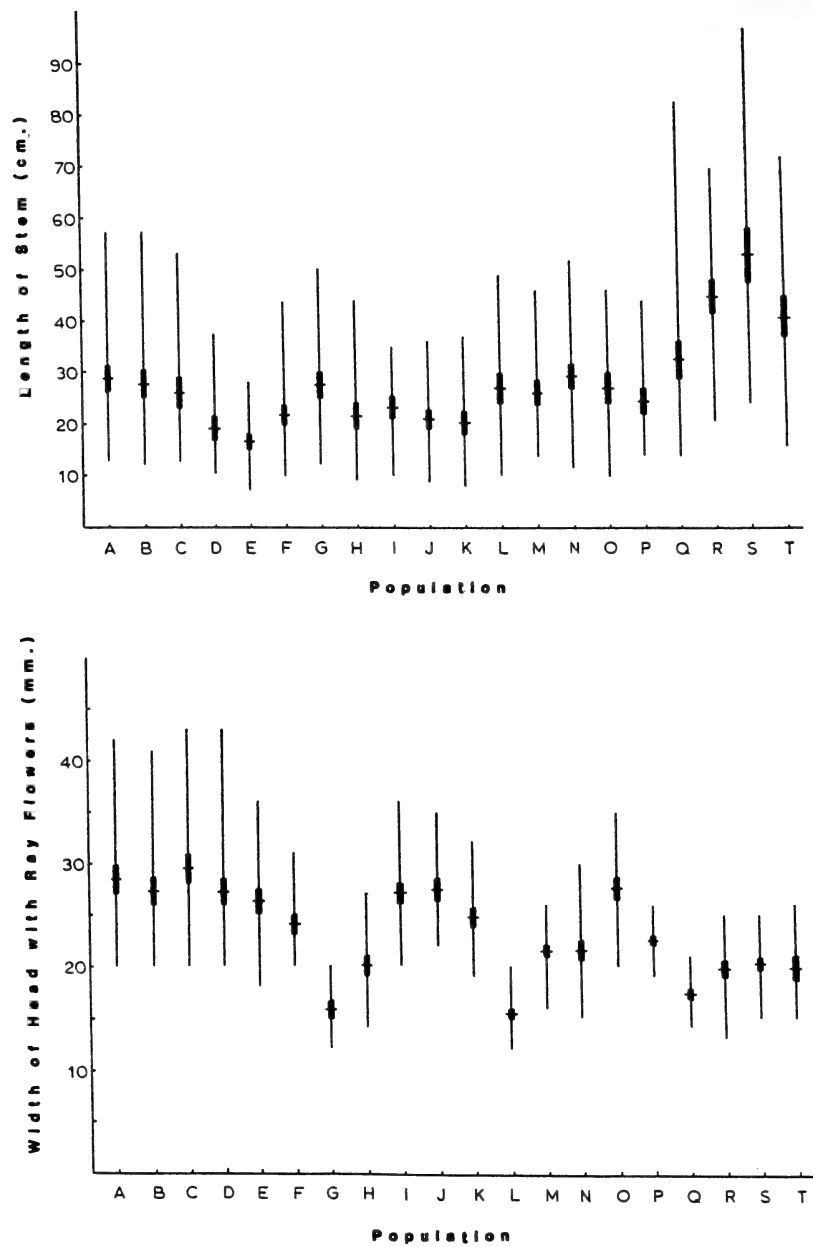
FIG. 2. Dice diagrams for variation (mean, ± two standard errors of the mean, and absolute range) in stem length and in width of head (cf. Fig. 1) in 20 populations (cf. appendix 1) of *Corethrogyne* (A–E = *C. filaginifolia* var. *californica*; F–T = *C. f.* var. *filaginifolia*).

As indicated in discussion above, we recognize two ± allopatric varieties within *C. filaginifolia*.

KEY TO VARIETIES OF *CORETHROGYNE FILAGINIFOLIA*

1. Floral stems usually branched, each with 3–6(1–20+) heads; lengths of involucres (fresh, at anthesis) 6–14 mm, mostly twice the diameters . . .
. . . . *C. filaginifolia* var. *filaginifolia*
1' Floral stems usually unbranched, each with 1(–5) heads; lengths of involucres (fresh, at anthesis) 5–

10 mm, about equal to diameters . . . .
. . . . *C. filaginifolia* var. *californica*

1. CORETHROGYNE FILAGINIFOLIA (Hook. & Arn.) Nutt. var. FILAGINIFOLIA.
Aster? *tomentellus* Hook. & Arn., Bot. Beechey voy. 146. 1833. ≡ *Corethrogyne tomentella* (Hook. & Arn.) Torrey & A. Gray, Fl. N. Amer. 2:99. 1841. ≡ *Corethrogyne californica* DC. [var.] *tomentella* (Hook. & Arn.) Kuntze, Rev.
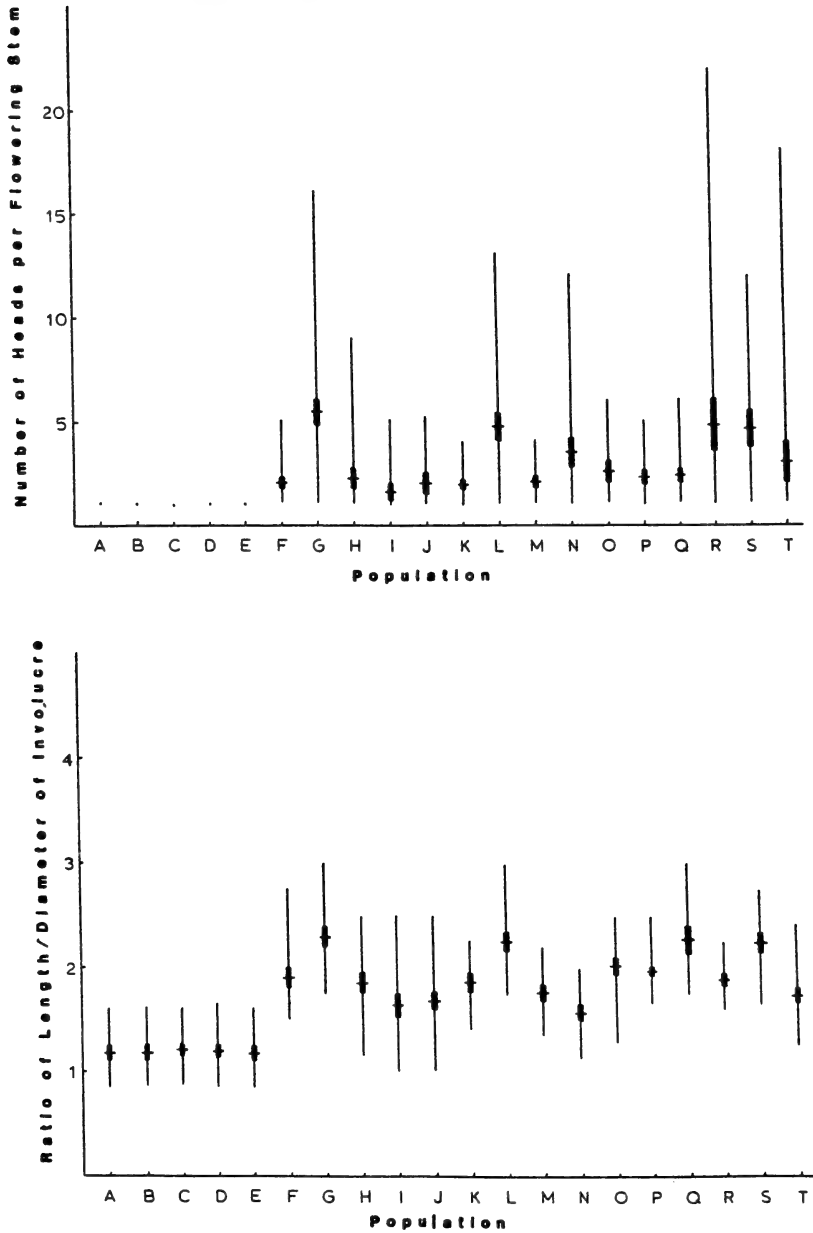
FIG. 3.   Dice diagrams for variation (mean, ± two standard errors of the mean, and absolute range) in numbers of heads per flowering stem and in ratio of length/diameter of involucre in 20 populations (cf. Appendix 1) of *Corethrogyne* (A–E = *C. filaginifolia* var. *californica*; F–T = *C. f.* var. *filaginifolia*).

gen. pl. 1:330. 1891 [illegit., oldest sp. epithet not used]. —Type: California, *F. W. Beechey et al. s.n.* (holotype: K!).

Diplopappus incanus Lindl., Edward's Bot. Reg. 20:1693. 1835. ≡ *Corethrogyne incana* (Lindl.) Nutt., Trans. Amer. Phil. Soc., ser 2. 7:290. 1840 [1841]. ≡ *Corethrogyne californica* DC. [var.] *incana* (Lindl.) Kuntze, Rev. gen. pl. 1:330. 1891 [illegit., oldest sp. epithet not used]. ≡ *Corethrogyne filaginifolia* (Hook. & Arn) Nutt. var. *incana* (Nutt.) M. L. Canby, Bull. S. Calif. Acad.

Sci. 26:14. 1927. —Type: California, *D. Douglas s.n.* (no specimen located; the plate confirms application of the name).

Aplopappus? *haenkei* DC., Prodr. 5:349. 1836. — Type: "inter plantas Regiomontanas herb. Haenkeani ab ill. de Sternberg ad studium missi conservatur"; specimens came from near Monterey, California, fide A. Gray (1876). Holotype may be in P; specimen in G-DC (microfiche!) confirms application of the name.

Diplopappus leucophyllus Lindl. ex DC., Prodr. 5:

278. 1836. ≡ *Corethrogyne californica* DC. [var.] *leucophylla* (Lindl. ex DC.) Kuntze, Rev. gen. pl. 1:330. 1891 [illegit., oldest sp. epithet not used]. ≡ *Corethrogyne leucophylla* (Lindl. ex DC.) Jeps. [attributed to Menzies], Fl. w. Calif. 564. 1901. —Type: California, Monterey Co., near Monterey, *A. Menzies s.n.* (holotype: K!).

Corethrogyne virgata Benth., Bot. voy. *Sulphur* 23. 1844. ≡ *Corethrogyne filaginifolia* (Hook. & Arn.) Nutt. var. *virgata* (Benth.) A. Gray in S. Watson, Bot. Calif. 1:321. 1876. ≡ *Corethrogyne californica* DC. [var.] *virgata* (Benth.) Kuntze, Rev. gen. pl. 1:330. 1891 [illegit., oldest sp. epithet not used]. —Type: California, San Pedro, *R. Hinds s.n.* (holotype: K!).

Corethrogyne incana (Lindl.) Nutt. var.? *rigida* Benth., Pl. hartweg. 316. 1849. ≡ *Corethrogyne filaginifolia* (Hook. & Arn.) Nutt. var. *rigida* (Benth.) A. Gray, Synop. fl. N. Amer. 1(2):170. 1884. ≡ *Corethrogyne californica* DC. [var.] *rigida* (Benth.) Kuntze, Rev. gen. pl. 1:330. 1891 [illegit., oldest sp. epithet not used]. ≡ *Corethrogyne rigida* (Benth.) A. Heller, Muhlenbergia 2:256. 1906. —Type: California, Monterey Co., "In collibus arenosis juxta Monterey," *K. T. Hartweg "1771(130)"* (holotype: K!).

Corethrogyne filaginifolia (Hook. & Arn.) Nutt. var. *robusta* Greene, Pittonia 1:89. 1887. —Lectotype (here designated): California, Santa Barbara Co., San Miguel Island, Sep 1886, *E. L. Greene s.n.* (lectotype: CAS!).

Corethrogyne viscidula Greene, Fl. francisc. 378. 1897. ≡ *Corethrogyne filaginifolia* (Hook. & Arn.) Nutt. var. *viscidula* (Greene) D. D. Keck, Aliso 4:105. 1958. —Type: California, Monterey Co., "Monterey," 22 Jul 1888, *C. C. Parry s.n.* (holotype: ND-G!).

Corethrogyne viscidula Greene var. *greenei* Jeps., Fl. w. Calif. 564. 1901. —Lectotype (here designated): California, Alameda Co., "Niles," 25 Jun 1896, *W. L. Jepson "14614"* (lectotype: JEPS!).

Corethrogyne virgata Benth. var. *bernardina* Abrams, Fl. Los Angeles 401. 1904. ≡ *Corethrogyne filaginifolia* (Hook. & Arn.) Nutt. var. *bernardina* (Abrams) H. M. Hall, Univ. Calif. Publ. Bot. 3:71. 1907. —Type: California, San Bernardino Co., Mentone, 10 Aug 1903, *L. Abrams 2931* (holotype: DS!).

Corethrogyne filaginifolia (Hook. & Arn.) Nutt. var. *glomerata* H. M. Hall, Univ. Calif. Publ. Bot. 3:72. 1907. —Type: California, San Bernardino Co., "Oak Glen, Yucaipe Ranch, near Redlands," Nov 1903, *G. Robertson 117* (holotype: UC!).

Corethrogyne filaginifolia (Hook. & Arn.) Nutt. var. *latifolia* H. M. Hall, Univ. Calif. Publ. Bot. 3:70. 1907. —Type: California, Ventura Co., Oxnard, 1901, *J. B. Davy 7815* (holotype: UC!).

Corethrogyne filaginifolia (Hook. & Arn.) Nutt.

var. *linifolia* H. M. Hall, Univ. Calif. Publ. Bot. 3:71. 1907. ≡ *Corethrogyne linifolia* (H. M. Hall) Ferris, Contr. Dudley Herb. 5:100. 1958. —Type: California, San Diego Co., ca. 1 km south of Del Mar, 5 Aug 1906, *K. Brandegee s.n.* (holotype: UC!).

Corethrogyne filaginifolia (Hook. & Arn.) Nutt. var. *pacifica* H. M. Hall, Univ. Calif. Publ. Bot. 3:73. 1907. —Type: California, San Diego Co., "Pacific Beach, near San Diego," May–Oct 1899, *C. A. Purpus s.n.* (holotype: UC!; isotype: US!).

Corethrogyne brevicula Greene, Leafl. Bot. Observ. Crit. 2:26. 1910. ≡ *Corethrogyne filaginifolia* (Hook. & Arn.) Nutt. var. *brevicula* (Greene) M. L. Canby, Bull. S. Calif. Acad. Sci. 26:12. 1927. —Type: California, "Mountains of San Diego Co.," Oct 1889 (label) or 1899 (protologue), *C. R. Orcutt s.n.* (holotype: US!).

Corethrogyne flagellaris Greene, Leafl. Bot. Observ. Crit. 2:26. 1910. —Type: California, Los Angeles Co., "Along the seaboard at Redondo," 25 May 1902, *E. Braunton 280* (holotype: US!; isotype: DS!).

Corethrogyne floccosa Greene, Leafl. Bot. Observ. Crit. 2:25. 1910. —Type: California, Santa Barbara Co., "Elwood, near Santa Barbara," Sep 1908, *A. Eastwood s.n.* (holotype: US!).

Corethrogyne lavandulacea Greene, Leafl. Bot. Observ. Crit. 2:27. 1910. —Type: California, Santa Catalina Island, Sep 1898, *B. Trask s.n.* (holotype: US!).

Corethrogyne racemosa Greene, Leafl. Bot. Observ. Crit. 2:26. 1910. —Type: California, "Mountains of San Diego Co.," Oct 1889, *C. R. Orcutt s.n.* (holotype: US!).

Corethrogyne scabra Greene, Leafl. Bot. Observ. Crit. 2:25. 1910. —Type: California, Los Angeles Co., Sep 1890, *H. E. Hasse s.n.* (holotype: US!).

Corethrogyne sessilis Greene, Leafl. Bot. Observ. Crit. 2:25. 1910. ≡ *Corethrogyne filaginifolia* (Hook. & Arn.) Nutt. var. *sessilis* (Greene) M. L. Canby, Bull. S. Calif. Acad. Sci. 26:15. 1927. —Type: California, "San Bernardino Mountains," 23 Oct 1891, *S. B. Parish 2233* (holotype: US!; isotype: UC!).

Corethrogyne filaginifolia (Hook. & Arn.) Nutt. var. *pinetorum* I. M. Johnst., Bull. S. Calif. Acad. Sci. 18:21. 1919. —Type: California, Los Angeles Co., San Antonio Mts., Brown's Flat, 1 Sep 1918, *I. M. Johnston 2137* (holotype: POM!; isotype: DS!).

Corethrogyne filaginifolia (Hook. & Arn.) Nutt. var. *peirsonii* M. L. Canby, Bull. S. Calif. Acad. Sci. 26:14. 1927. —Type: California, Los Angeles Co., Newhall, 7 Oct 1923, *F. W. Peirson 4159* (holotype: POM!; isotype: DS!).

Corethrogyne filaginifolia (Hook. & Arn.) Nutt. var. *hamiltonensis* D. D. Keck, Aliso 4:105. 1958. —Type: California, Santa Clara Co., Mt.

Hamilton, Aug 1914, *H. M. Hall 9865* (holotype: NY!).

Primary stems predominately erect, mostly 1–10 dm long, usually branched distally. Leaf blades narrowly spatulate to linear, entire or toothed. Heads (1–)5–20+ per floral stem. Involucres cylindric to turbinate, lengths (6–14 mm) mostly twice diameters (3–8 mm) at anthesis in living plants. Phyllaries mostly 4–9-seriate. Disc florets mostly 12–40, corollas mostly 4-6 mm long.

Widespread through much of cismontane California from Placer Co. south through Sierra Nevada and in interior mountains of Contra Costa and Alameda cos. south through coast ranges to transverse ranges and Channel Islands and into northern Baja California.

2. **Corethrogyne filaginifolia** (Hook. & Arn.) Nutt. var. **californica** (DC.) Saroyan, comb. nov. ≡ *Corethrogyne californica* DC., Prodr. 5:215. 1836. ≡ *Lessingia filaginifolia* (Hook. & Arn.) M. A. Lane var. *californica* (DC.) M. A. Lane, Novon 2:213. 1992. —Type: "Nova California," 1833, *D. Douglas s.n.* (holotype: G-DC, microfiche!; isotypes: BM!, K!).
Corethrogyne obovata Benth., Bot. voy. *Sulphur* 22. 1844. ≡ *Corethrogyne californica* DC. [var.] *obovata* (Benth.) Kuntze, Rev. gen. pl. 1:330. 1891 [illegit., oldest sp. epithet not used]. —Type: California, "Bodegas," 1841, *R. Hinds s.n.* (holotype: K!).
Corethrogyne spathulata A. Gray, Proc. Amer. Acad. Arts 7:351. 1868. ≡ *Corethrogyne californica* DC. [var.] *spathulata* (A. Gray) Kuntze, Rev. gen. pl. 1:330. 1891 [illegit., oldest sp. epithet not used]. —Type: California, Humboldt Co., Shelter Cove, 1867, *H. N. Bolander 6505* (holotype: GH!; isotypes: BM!, K!, US!).
Corethrogyne caespitosa Greene, Fl. francisc. 378. 1897. —Type: California, San Mateo Co., Crystal Springs, 22 Jun 1886, *E. L. Greene s.n.* (holotype: ND-G!; isotypes: PH!, US!).
Corethrogyne californica DC. var. *lyonii* S. F. Blake, J. Wash. Acad. Sci. 33:267. 1943. —Type: California, Merced Co., Cathedral Peak, 4 Jun 1941, *G. S. Lyon 1572* (holotype: US!, formerly in NA; isotypes: DS!, UC!).

Primary stems predominately decumbent to ascending, mostly less than 6 dm long, mostly unbranched. Leaf blades mostly obovate to spatulate, toothed. Heads mostly 1(–5) per floral stem. Involucres hemispheric to campanulate, lengths (5–10 mm) mostly equalling diameters at anthesis in living plants. Phyllaries mostly 3–5-seriate. Disc florets 30–120+, corollas mostly 6–8 mm long.

Common as discrete, very local, usually dense populations from northern Monterey, San Benito, and western Merced cos. north through the North Coast Ranges of California into western Klamath Range in Coos Co., Oregon.

QUESTIONABLE NAME AND EXCLUDED TAXA

Corethrogyne californica DC. [var.] *recurva* Kuntze, Rev. gen. pl. 1:330. 1891 [illegit., oldest sp. epithet not used]. —Type: We have not seen type material; the description, "Involucri bracteae apice recurvae," is insufficient to allow confident application of the name.
Corethrogyne cana (A. Gray) Greene, Bull. Calif. Acad. Sci. 1(no. 4):223. 1885. ≡ *Diplostephium canum* A. Gray, Proc. Amer. Acad. Arts 11:75. 1876. ≡ HAZARDIA CANA (A. Gray) Greene, Pittonia 1:29. 1887. ≡ *Haplopappus canus* (A. Gray) S. F. Blake, Contr. U.S. Natl. Herb. 24:86. 1922. —Type: Mexico, Baja California, Guadalupe Island, 28 Mar 1875, *E. Palmer s.n.* (holotype: GH).
Corethrogyne detonsa Greene, Bull. Torrey Bot. Club 10:41. 1883. ≡ HAZARDIA DETONSA (Greene) Greene, Pittonia 1:29. 1887. ≡ *Haplopappus detonsus* (Greene) P. H. Raven, Aliso 5:343. 1963. —Type: Origin and collector unknown (holotype: CAS!).

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APPENDIX 1. STUDY POPULATIONS OF *CORETHROGYNE*. Order of entries is north to south. Each entry follows the form: **alphabetic identifier**; latitude; longitude; elevation (m); distance from ocean (km); vegetation (grasslands, coastal scrub, chaparral, forest); geographic location (all in California); and average pollen stainability (number of plants sampled for pollen stainability). Chromosome counts for one or more plants from each of the populations all yielded $2n = 5$ II. Voucher collections are in UC.

A. 41°47′; 124°08′; 75 m; 0.4 km; grasslands; Humboldt Co., 2.5 miles north of Patricks Point; 90%(4). **B.** 38°57′; 123°43′; 75 m; 0.04 km; grasslands; Mendocino Co., 500 yards east of Point Arena; 88%(7). **C.** 38°08′; 122°53′; 75 m; 4.8 km; grasslands; Marin Co., along Pierce Point Road, 1 mile south of Tomales Bay State Park; 87%(5). **D.** 38°05′; 122°45′; 200 m; 9.5 km; grasslands; Marin Co., on Inverness Ridge, 3 miles west of Inverness; 93%(7). **E.** 37°30′; 122°20′; 100 m; 11.25 km; grasslands; San Mateo Co., east bank of Upper Crystal Springs Reservoir 0.25 mile south of highway 92; 97%(11). **F.** 36°42′; 121°48′; 25 m; 0.4 km; grasslands; Monterey Co., 0.25 miles east of ocean, 1 mile south of animal shelter on dunes of Marina Beach; 93%(7). **G.** 36°38′; 121°46′; 125 m; 4.8 km; chaparral; Monterey Co., Fort Ord, break area of M-79 grenade range 83%(1). **H.** 36°37′; 121°56′; 10 m; 0.02 km; grasslands; Monterey Co., 1 mile north of limit of Asilomar Beach; 93%(13). **I.** 36°35′; 121°58′; 10 m; 0.03 km; grasslands; Monterey Co., opposite Seal Rock on 17-Mile Drive; 91%(2). **J.** 35°34′; 121°59′; 25 m; 0.03 km; forest; Monterey Co., opposite Cypress Point on 17-Mile Drive; 94%(9). **K.** 36°30′; 121°55′; 10 m; 0.02 km; grasslands; Monterey Co., vacant lot at Yankee Point, 1 mile south of Point Lobos; 80%(4). **L.** 36°23′; 121°30′; 40 m; 35.5 km; chaparral; Monterey Co., Hastings Reservation, along trail between bunk houses; 84%(5). **M.** 36°17′; 121°51′; 25 m; 0.8 km; grasslands; Monterey Co., along highway 1, 10 miles south of Point Lobos; 93%(5). **N.** 36°16′; 121°50′; 250 m; 0.8 km; coastal scrub; Monterey Co., coastal bluff, 0.25 mile west of highway 1, 15 miles south of Carmel; 92%(12). **O.** 35°52′; 121°27′; 300 m; 0.5 km; grasslands; Monterey Co., 1.2 miles north of Gorda; 94%(2). **P.** 35°39′; 121°14′; 10 m; 0.02 km; grasslands; San Luis Obispo Co., 3 miles north of San Simeon; 91%(3). **Q.** 34°56′; 120°38′; 150 m; 3 km; grasslands; Santa Barbara Co., 3 miles east of Point Sal; 85%(1). **R.** 34°35′; 120°25′; 100 m; 14.5 km; grasslands; Santa Barbara Co., 1 mile south of Lompoc, 0.5 mile west of highway 1; 98%(2). **S.** 34°13′; 117°12′; 2000 m; 100 km; forest; San Bernardino Co., 3 miles south of Lake Arrowhead, 0.5 miles west of highway 18; 86%(4). **T.** 33°00′; 117°15′; 200 m; 0.8 km; coastal scrub; San Diego Co., coastal bluff near Torrey Pines State Reserve; 90%(3).

CORRESPONDENCE BETWEEN NI TOLERANCE AND HYPERACCUMULATION IN *STREPTANTHUS* (BRASSICACEAE)

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ABSTRACT

Nickel hyperaccumulation may be associated with increased Ni tolerance for some plant species that grow on serpentine soils. We contrasted the Ni tolerance of three species: a Ni hyperaccumulator (*Streptanthus polygaloides* A. Gray) endemic to serpentine soil, a congeneric non-hyperaccumulator also endemic to serpentine soil (*S. breweri* A. Gray), and a species from the same family but not adapted to serpentine soil (*Brassica oleracea* L.). We assessed Ni tolerance by measuring germination and radicle elongation in test solutions varying in Ni^{+2} content. By both approaches, Ni tolerance was greatest for the hyperaccumulator, intermediate for the non-hyperaccumulator, and least for the unadapted species. A soil-based test of root elongation, using *S. polygaloides* and *B. oleracea* with two serpentine soils and one non-serpentine soil, showed a significant species-by-soil interaction. Root elongation of *B. oleracea* was inhibited in serpentine soil, whereas *S. polygaloides* showed reduced root elongation in non-serpentine soil. We concluded that these results are consistent with the hypothesis that Ni hyperaccumulation is a metal tolerance mechanism adopted by some species native to serpentine soils. These results also are consistent with other ecological functions of Ni hyperaccumulation, such as the elemental allelopathy or microsite tolerance hypotheses.

Plant tissues vary widely in heavy metal concentrations, although most plant species contain very low levels. Pais and Jones (1997) reported that species not adapted to high-Ni soils typically contain 0.3–3.5 μg Ni/g dry wt. For these species, tissue Ni in the range 8–50 μg/g dry wt usually denotes a toxic Ni concentration (MacNicol and Beckett 1985).

Serpentine soils often contain elevated levels of Ni (Kruckeberg 1984; Brooks 1987). Many plants native to these soils also contain elevated levels of Ni (Reeves 1992), often ranging from 10–100 μg Ni/g (Brooks 1987). Baker and Walker (1990) called these species "accumulators". A small proportion of plant species native to serpentine soils accumulate Ni to an extraordinary degree over a wide range of soil Ni concentrations (Morrison et al. 1980). Brooks et al. (1977) termed these plants "hyperaccumulators", defining them as containing at least 1000 μg Ni/g.

Many workers have suggested that metal hyperaccumulation has an adaptive function. Metal hyperaccumulators belong to a number of evolutionary lines of dicotyledonous plants (Brooks 1987), suggesting multiple independent evolution of this trait and therefore that metal hyperaccumulation has positive selective value. Boyd and Martens (1992) suggested four functions of metal hyperaccumulation: metal tolerance, drought tolerance/avoidance, defense against herbivores/pathogens, and interference with neighboring plants. To date most research has focused on defensive explanations (Boyd 1998). This work has shown that hyperaccumulated metals can defend plants against herbivores (Boyd and Martens 1994; Martens and

Boyd 1994; Pollard and Baker 1997; Sagner et al. 1998; Boyd and Moar 1999; Davis 1999; Jhee et al. 1999) and pathogens (Boyd et al. 1994; Ghaderian et al. 2000). The remaining hypothesized functions of metal hyperaccumulation are relatively unexplored.

Metal hyperaccumulation has been suggested to function as a mechanism for tolerating elevated soil metal contents (Boyd and Martens 1992). Metals could be removed from metabolically sensitive areas of a plant's cells or tissues by concentrating them in less sensitive locations (e.g., vacuoles, cell walls, epidermal cells, and trichomes). In some cases (e.g., Ernst 1972; Wild 1978), it has been proposed that abscission or loss of high-metal plant parts serves to dispose metals from the plant body. The difficulty with this "tolerance hypothesis" (*sensu* Boyd and Martens 1992) is that, although metal hyperaccumulators must surely be able to tolerate very high tissue metal levels, there is no evidence that tolerance is an adaptive function of metal hyperaccumulation. Thus, it is important to compare the metal tolerances of hyperaccumulator and non-hyperaccumulator species native to serpentine soils. If both have equivalent metal tolerance abilities, then this would be evidence contrary to the tolerance hypothesis.

Increased metal tolerance of hyperaccumulator species relative to other species able to grow on serpentine soil is also crucial to the "interference hypothesis" (*sensu* Boyd and Martens 1992). Some authors (e.g., Gabbrielli et al. 1991; Baker et al. 1992) have suggested that the elevated metal content of leaf litter produced by hyperaccumulators can lead to increased metal content of the surface

soil beneath individual plant canopies. Less metal-tolerant species may be prevented from growing in these metal-enriched areas, resulting in lessened competition for the hyperaccumulator. Wilson and Agnew (1992) further suggested that metal hyperaccumulators might suppress the growth of less metal-tolerant species through surface soil metal enrichment and thus create areas dominated by relatively pure stands of the hyperaccumulator species. This interaction was termed ''elemental allelopathy'' by Boyd and Martens (1998), due to the similarity of this phenomenon with allelopathy (Rice 1984). Boyd and Martens (1998) pointed out that experimental confirmation of elemental allelopathy must demonstrate two facts. First, soil Ni levels must be significantly elevated in the vicinity of hyperaccumulator plants, relative to other microsites in serpentine habitats. Second, it must be demonstrated that hyperaccumulator species are more metal tolerant than potentially competing species. Thus, demonstration of differential metal tolerance between hyperaccumulator and non-hyperaccumulator serpentine species is one of the two principles essential to uphold the elemental allelopathy hypothesis.

As explained above, both the tolerance hypothesis and the elemental allelopathy (interference) hypothesis require that metal hyperaccumulators be more metal-tolerant than other serpentine soil species. Some studies of hyperaccumulators (e.g., Kramer et al. 1997) have contrasted them with a congener that is not native to metalliferous soils and several studies have compared the metal tolerance of hyperaccumulator species with other species. The early work of Morrison et al. (1980) examined the Ni tolerances of seven Ni-hyperaccumulating species and two non-hyperaccumulating species of *Alyssum*. Root elongation tests showed the hyperaccumulators to be more Ni tolerant than non-hyperaccumulators. Gabbrielli et al. (1990) used root elongation tests to contrast the Ni tolerance of the hyperaccumulator *A. bertolonii* Desv. with that of the non-hyperaccumulator serpentine species, *Silene italica* L., and showed that the hyperaccumulator was much more Ni tolerant than the non-hyperaccumulator. Homer et al. (1991) contrasted a Ni hyperaccumulator (*Alyssum troodii* Boiss.) and a non-hyperaccumulator (*Alyssum saxatilis* = *Aurinia saxatilis* (L.) Desv.), finding greater Ni tolerance for the hyperaccumulator by examining both biomass production and germination experiments. Kramer et al. (1996) obtained similar results, using a non-hyperaccumulating *Alyssum* species (*A. montanum*) and contrasting its Ni tolerance with the Ni hyperaccumulator *A. lesbiacum*. Biomass production of the Ni hyperaccumulator was much greater than the non-hyperaccumulator when plants were grown in a series of Ni-containing solutions. Shen et al. (1997) studied Zn tolerance of two serpentine soil species of *Thlaspi* by measuring biomass accumulation as a function of Zn concentration in the growth medium. They found that the Zn hyperaccumulator *T. caerulescens* was more Zn tolerant than the non-hyperaccumulator *T. ochroleucum.*

The research reported here was conducted to compare the Ni tolerance of two annual species of *Streptanthus,* both of which are endemic to serpentine soils, but only one is a Ni hyperaccumulator. This New World genus in the Brassicaceae contains a single Ni hyperaccumulator species, *S. polygaloides* A. Gray, and a number of non-hyperaccumulating taxa endemic to serpentine soils (Kruckeberg 1984). *Streptanthus polygaloides* also is unique among hyperaccumulators due to its being an obligate annual. Other Ni hyperaccumulators, including those in *Alyssum* and *Thlaspi,* are perennials and thus the present work extends our understanding of the relationship between hyperaccumulation and tolerance to annual species in another genus.

METHODS

Study species. Streptanthus polygaloides is an annual Ni hyperaccumulator endemic to serpentine soils in the western foothills of the Sierra Nevada in California (Munz and Keck 1968). Studies by Reeves et al. (1981) and Kruckeberg and Reeves (1995) have documented >1000 µg Ni/g dry wt in all parts of this species. We collected seeds from the Red Hills of Tuolumne County, California (Favre 1987), approximating sample #6737 of Kruckeberg and Reeves (1995).

We selected *S. breweri* A. Gray to represent a non-hyperaccumulating species of *Streptanthus.* This species also is an annual and is also endemic to serpentine soils (Kruckeberg 1984). The ranges of these two species do not overlap because *S. breweri* is native to the Coast Ranges of California (Munz and Keck 1968). Analysis of leaves of this species by Kruckeberg and Reeves (1995) showed a maximum of 13 µg Ni/g. Specimens analyzed by Reeves et al. (1981) contained <9 µg Ni/g. We collected seeds from a population in Napa County, California, near sample #6742 of Kruckeberg and Reeves (1995).

The third species used was broccoli, *Brassica oleracea* L. This species is also in the Brassicaceae, but is not adapted to serpentine soil. Seeds were obtained from a commercial source.

Germination tests. Seeds were placed in 5-cm diameter petri dishes under 24-hr illumination at room temperature. Germination solutions were added in sufficient quantity to completely cover seeds, and were replenished as needed during the experiments. Nickel concentrations used for seeds of *S. polygaloides* and *S. breweri* were 0, 4.3, 8.5, 13, 17, 26, 34, 43, 51, and 60 mmol/L. The experiment using *B. oleracea* seeds used fewer Ni^{+2} concentrations, 0, 8.5, 13, 17, 34, and 51 mmol/L, because we assumed the Ni^{+2} tolerance of this unadapted species would be easier to characterize. Nickel was

supplied as $NiCl_2$ (Fisher Scientific). The use of $NiCl_2$ presented the possibility that inhibition could occur due to increased Cl^{-1} ion concentration rather than Ni^{+2}. To test for this effect (as well as osmotic effects) on seed germination, solutions containing 0, 12, 19, 25, 50, 75, 100, 125, 150, 175, 200, 225, and 250 mmol Ca^{+2}/L (as $CaCl_2$, Fisher Scientific) were used. Seeds of two species, *S. polygaloides* and *B. oleracea,* were used for Ca^{+2} experiments. Due to insufficient seed availability, these experiments were not conducted using *S. breweri* seeds.

Seeds (ranging in number between 10 and 15) of each species were placed in each petri plate and monitored for germination (defined as emergence of the radicle from the seed coat) until germination declined to zero during a several-day period. Ten petri plates (replicates) were used for each combination of species, Ni^{+2}, and Ca^{+2} concentration. Germinating seeds were removed from petri plates to minimize their influence on the chemistry of the germination solutions. Percent germination was calculated for the seeds in each petri plate and these data were analyzed by one-way ANOVA for each species and each ion (Ni^{+2} or Ca^{+2}) used, after transformation (arcsine square root) so data would better fit ANOVA assumptions (Zar 1996). Fisher's Protected Least Significant Difference (PLSD) test (Abacus Concepts 1992) was used for post-hoc means separation ($\alpha \le 0.05$).

Root elongation tests in solution. Seeds of all three species were placed on moistened filter paper in petri dishes and allowed to germinate. Once radicles reached lengths of 1–3 mm, seedlings were removed and transferred to root elongation test solutions. At least three seedlings (up to five if more were available) were used in each petri plate. Three petri plates (replicates) of each species were used for each concentration of Ca^{+2} or Ni^{+2}. Radicles of transplanted seedlings were allowed to elongate for 7 d at room temperature, after which they were removed from test solutions and the length of the primary root measured.

All test solutions contained a background level of ions important for normal seedling development (Baker 1987). The background solution contained 0.77 mmol Ca^{+2}/L as $Ca(NO_3)_2$, 0.82 mmol Mg^{+2}/L as $MgSO_4$, and 0.28 mmol K^{+1}/L as KNO_3 (all obtained from Fisher Scientific). $NiCl_2$ was then added to the background solution to create concentrations of 0, 0.085, 0.17, 0.34, 0.51, 0.68, 0.85, 1.4, and 1.7 mmol Ni^{+2}/L.

As in the germination experiment, the addition of Cl^{-1} along with Ni^{+2} presented the possibility that inhibition could occur due to increased Cl^{-1} concentration rather than Ni^{+2}. To test for this effect (and general osmotic effects), three Ca^{+2} solutions were created with $CaCl_2$, using the same background solution used for the Ni^{+2} experiments, to create solutions containing 2.5, 5.0, or 10 mmol Ca^{+2}/L.

Root lengths from seedlings in each petri plate were averaged, and the data analyzed by one-way ANOVA for each species and solution type (Ni^{+2} or Ca^{+2}) after log-transformation so data would better fit ANOVA assumptions (Zar 1996). Fisher's PLSD test was used for post-hoc means separation ($\alpha \le 0.05$).

Root elongation tests in soil. This experiment determined if the tolerance results from Ni^{+2} solutions had relevance to root performance in serpentine soils. Three soils were used for testing root elongation: two from serpentine sites in California and one from a non-serpentine site in Alabama. The first serpentine soil was collected from the Red Hills in Tuolumne County. The second was collected from a serpentine site along U.S. Highway 101 near the southern city limit of San Luis Obispo, San Luis Obispo County, California. The non-serpentine soil was collected from Auburn, Lee County, Alabama. Approximately 1 L of soil was collected to 10 cm depth at each location and sieved to remove stones >2 mm dia.

A subsample of each soil was used for elemental analysis. Soil samples were double-acid extracted using 20 mL of extractant (0.05 M HCl/0.025 M H_2SO_4) shaken with 5 g of dry soil for 5 min. The extract was analyzed for Ni using an atomic absorption spectrophotometer (IL 251, Instrumentation Laboratory, Franklin, MA), and for Ca, K, Mg, P, Cu, Fe, Mn, Cr, Pb, Co and Zn using an inductively-coupled argon plasma spectrometer (ICAP 9000, Jarrell-Ash, Franklin, MA).

Soil from each location was put into small (5 cm diam.) petri plates to approx. 5 mm depth and moistened with deionized water. Seeds of two species, the unadapted *B. oleracea* and the hyperaccumulator *S. polygaloides,* were used (not enough seeds of *S. breweri* were available). Seeds were germinated on moist filter paper. Germinating seeds (radicles 1–3 mm long) were transferred to the surface of the soil plates and allowed to grow for 4 d. Three seedlings were used for each replicate, and radicle lengths were averaged for each plate. Seedlings of these two species differed in size, so that direct comparisons of root length were confounded by this factor. We minimized the influence of this innate size difference by relativizing mean root lengths for each species within a replicate. Means were expressed as a decimal fraction of the mean for that treatment which produced the largest mean root length. Mean root lengths for each of the three treatments were each divided by the largest value of those three data, resulting in a value of 1 for the largest mean and lesser values for the other two means. These relativized data were analyzed by two-way ANOVA, using transformed (arcsine square root) data to better meet the assumptions of ANOVA (Zar 1996). Soil collection site and species were main effect factors and the interaction term was included in the ANOVA model. Fisher's

Protected Least Significant Difference (PLSD) test (Abacus Concepts 1992) was used for post-hoc means separation ($\alpha \leq 0.05$).

RESULTS

Germination tests. Germination of all three species was significantly affected by Ni^{+2} concentration. For *S. polygaloides,* ANOVA indicated a significant Ni^{+2} effect ($F_{9,90} = 21$, $P < 0.0001$). Germination was relatively high (>50%) for even the most concentrated (60 mmol/L) solution (Fig. 1), and Fisher's PLSD test indicated that germination was equivalent to that of the control for all solutions containing <17 mmol/L. *Streptanthus breweri* germination also was significantly affected by Ni^{+2} (ANOVA: $F_{9,89} = 22$, $P < 0.0001$). Germination was less than 50% for the higher Ni^{+2} concentrations (>34 mmol/L), and a significant decline in germination relative to the control (Fisher's PLSD test) was first observed at a lesser concentration than for *S. polygaloides* (13 mmol/L vs. 17 mmol/L: Fig. 1). *Brassica oleracea* germination also declined significantly as Ni^{+2} concentration increased (ANOVA: $F_{5,54} = 38$, $P < 0.0001$). Germination declined to <50% at concentrations >8.5 mmol Ni^{+2}/L, with Fisher's PLSD test showing that germination first declined significantly relative to the control at 8.5 mmol Ni^{+2}/L.

Experiments with Ca^{+2} solutions also showed inhibition of germination for all species (data not shown), but at greater concentrations than with Ni^{+2} solutions. Germination of *S. polygaloides* was significantly affected by Ca^{+2} concentration (ANOVA: $F_{12,117} = 110$, $P < 0.0001$). Mean germination was >75% for those solutions containing up to 50 mmol Ca^{+2}/L, but declined significantly compared to the control (Fisher's PLSD test), reaching 37% at 75 mmol/L. Germination of *B. oleracea* also was significantly affected by Ca^{+2} concentration (ANOVA: $F_{12,117} = 67$, $P < 0.0001$). Mean germination was >72% for concentrations up to 75 mmol Ca^{+2}/L, and then declined significantly relative to the control (Fisher's PLSD test) to 64% at 100 mmol/L. These results show that Cl^{-1} did not produce the decreased germination observed with the Ni^{+2} solutions, and that Ni^{+2} played a significant role in decreasing seed germination in this experiment.

Root elongation tests in solution. Solution Ni^{+2} concentration significantly affected root elongation for all species tested. For *S. polygaloides,* ANOVA showed a significant Ni^{+2} effect ($F_{8,63} = 29$, $P < 0.0001$). Mean root length declined significantly relative to the control at 0.085 mmol Ni^{+2}/L (Fisher's PLSD test, Fig. 2). Maximum inhibition (smallest mean root elongation) was observed at the highest Ni^{+2} concentration used (1.7 mmol Ni^{+2}/L). Comparing means to that value, the lowest concentration of Ni^{+2} that resulted in maximum inhibition was 0.85 mmol/L (Fisher's PLSD test). This value begins the maximum inhibition zone noted on Fig-
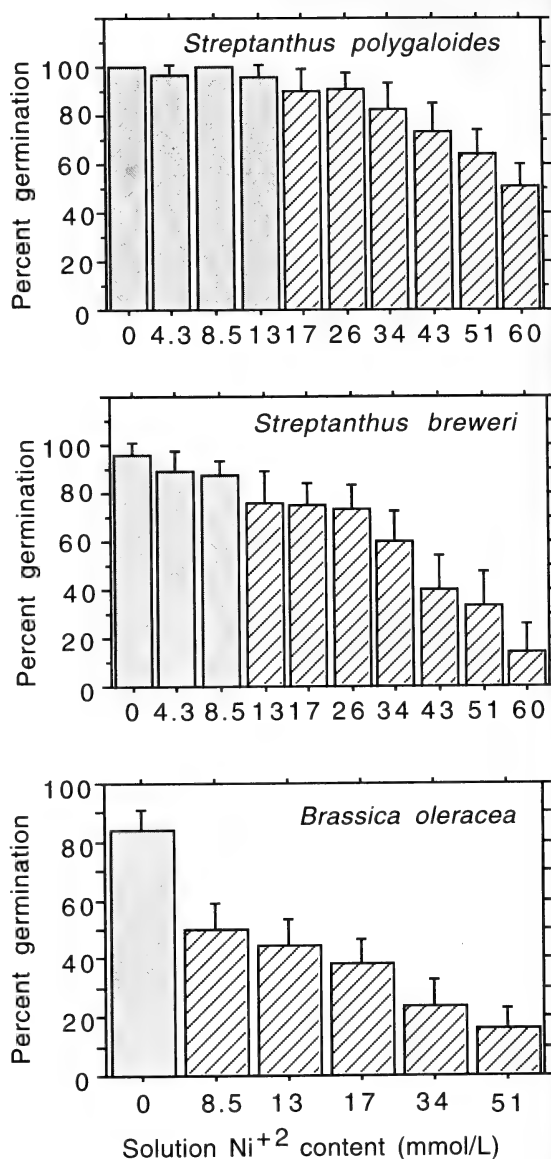
FIG. 1. Percent germination of the three experimental species as influenced by Ni^{+2} content of the germination test solution. Note that the x-axes are not linear. The hatched bars in each graph indicate treatments for which germination was lowered significantly from that of the control (0 mmol Ni^{+2}/L) treatment. Error bars denote the upper 95% confidence limit of each mean.

ure 2, and represents the lowest Ni^{+2} level that causes maximum root growth inhibition. Root growth of *S. breweri* also declined with increasing Ni^{+2} concentration (ANOVA: $F_{8,63} = 84$, $P < 0.0001$). Again, means declined significantly relative to the control at 0.085 mmol/L (Fisher's PLSD test, Fig. 2). In this case, however, the maximum inhibition zone began at a lesser Ni concentration than for *S. polygaloides.* For *S. breweri,* the maximum inhibition zone started at 0.51 mmol Ni^{+2}/L
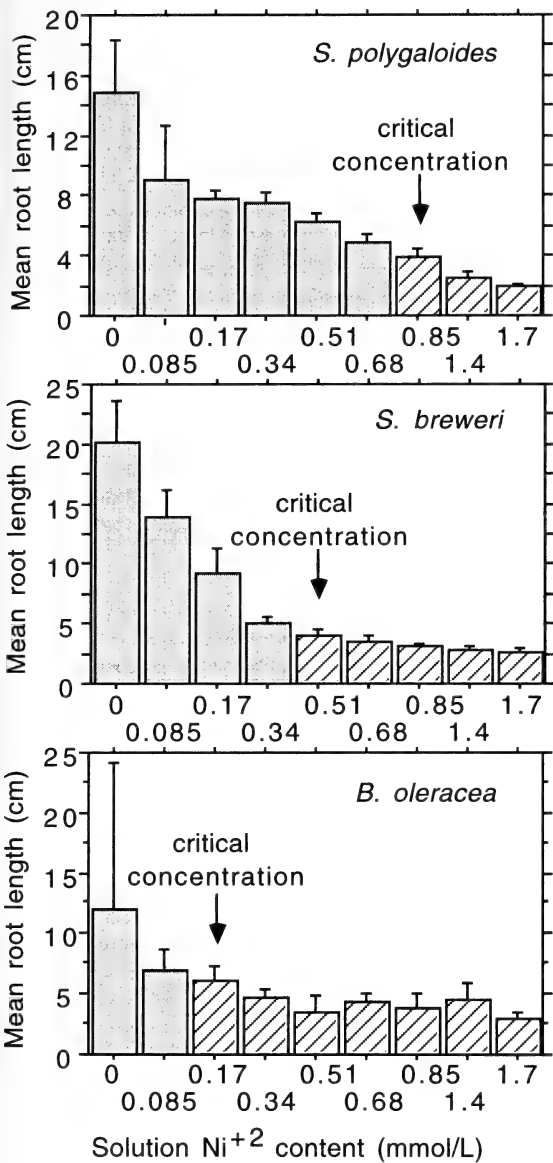
FIG. 2.   Mean root lengths (cm) of seedlings of the three experimental species as affected by solution Ni^{+2} concentration. The hatched bars denote treatments that resulted in maximum inhibition of root elongation (all hatched bars are not statistically different from the 1.7 mmol Ni^{+2}/L solution, using Fisher's PLSD test). Error bars denote the upper 95% confidence limit of each mean.

FIG. 3.   Mean root lengths (cm) of seedlings of the three experimental species as affected by solution Ca^{+2} concentration. Error bars denote the upper 95% confidence limit of each mean.

(Fisher's PLSD test comparison with mean value at 1.7 mmol/L, Fig. 2). Root growth of *B. oleracea* also was significantly depressed by Ni^{+2} solutions (ANOVA: $F_{8,27}$ = 4.3, P = 0.0021). Mean root elongation again declined significantly at 0.085 mmol Ni^{+2}/L (Fisher's PLSD test, Fig. 2), but the maximum inhibition zone began at the lowest Ni concentration for all three species tested. For *B. oleracea,* the maximum inhibition zone extended

from 0.17–1.7 mmol/L (Fisher's PLSD test comparison with mean at 1.7 mmol/L, Fig. 2).

Effects of the Ni^{+2} solutions on root elongation did not result from Cl^{-1} or overall osmotic concentrations of the test solutions. For all species tested, root elongation in $CaCl_2$ solutions was not significantly depressed relative to control solutions at the highest concentration tested (10 mmol/L, Fig. 3). The Cl^{-1} concentration of the 10 mmol Ca^{+2}/L solution was much higher than that of the highest (1.7 mmol/L) Ni^{+2} solution. Thus, a Cl^{-1} effect cannot explain the significant declines of root elongation observed for all species tested with the 0.085 mmol Ni^{+2}/L solution. However, a significantly positive
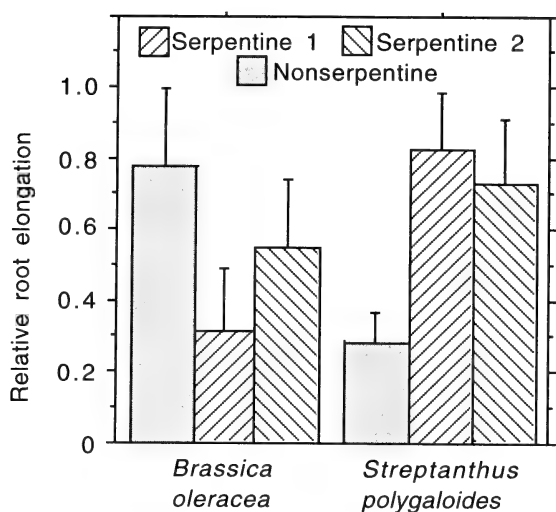
FIG. 4. Mean relative root elongation of *B. oleracea* and *S. polygaloides* on three soil treatments (two serpentine and one non-serpentine soil). Error bars denote the upper 95% confidence limit of each mean.

TABLE 1. ELEMENTAL ANALYSIS OF THE THREE SOILS USED IN THE SOIL ROOT ELONGATION TESTS. Serpentine Soil 1 was collected from the Red Hills, Tuolumne County, California, Serpentine Soil 2 was collected from San Luis Obispo County, California, and the Non-serpentine Soil came from Auburn, Lee County, Alabama.

Parameter ($\mu g \ g^{-1}$)	Serpentine Soil 1	Serpentine Soil 2	Non-serpentine Soil
Ca	200	1960	484
K	33.2	15.6	16.8
Mg	493	742	59.0
P	5.10	17.8	60.2
Cu	0.23	0.991	1.41
Mn	27.6	56.1	20.4
Zn	0.92	4.82	53.0
Co	1.72	4.47	0.14
Cr	0.12	1.21	0.085
Pb	0.443	11.4	12.8
Ni	80	128	<4
Ca/Mg ratio	0.41	2.6	8.2

effect of Ca^{+2} was detected for two of the three species. *Streptanthus breweri* was the one species that lacked a significant Ca^{+2} effect (ANOVA: $F_{3,28}$ = 2.5, P = 0.0803). *Streptanthus polygaloides* showed a significant Ca^{+2} effect (ANOVA: $F_{3,28}$ = 8.2, P = 0.0004). Fisher's PLSD test revealed that root elongation for the 2.5 mmol Ca^{+2}/L solution was greater than for any other test solution. *Brassica oleracea* also showed a significant effect (ANOVA: $F_{3,12}$ = 12, P = 0.006). In this case, Fisher's PLSD test showed that root elongation for the control treatment was significantly lower than for the solutions with elevated Ca^{+2}. In all cases, a significant decline in root elongation (either due to Cl^{-1} or osmotic effects) was not observed with the Ca^{+2} solutions used. Thus, we conclude that the inhibitory effects of the Ni^{+2} solutions were attributable to Ni^{+2}.

Root elongation tests in soil. Relativized root elongation values were not significantly affected by either of the two main effect factors (soil and species) in the ANOVA (for soil: $F_{2,72}$ = 0.40, P = 0.67, and for species: $F_{1,72}$ = 0.86, P = 0.36). However, the interaction term was highly significant ($F_{2,72}$ = 21, P < 0.0001). Inspection of mean relative root elongation values revealed that the two species reacted in opposite ways to the soils (Fig. 4). *Brassica oleracea* root elongation was greatest in the non-serpentine soil (mean = 0.78), and less in both of the serpentine soils (Serpentine Soil 1 mean = 0.32; Serpentine Soil 2 mean = 0.55). Fisher's PLSD test showed that the mean for roots from the non-serpentine soil was significantly greater than for roots from Serpentine Soil 1, but the other pairwise comparisons were only marginally significant (P = 0.072 for each). On the other

hand, *S. polygaloides* showed depressed root elongation in the non-serpentine soil (mean = 0.29) and higher root elongation in both serpentine soils (Serpentine Soil 1 mean = 0.83; Serpentine Soil 2 mean = 0.73). Fisher's PLSD test showed that the mean for roots from non-serpentine soil was significantly less than for both serpentine soils (P < 0.0001 for both comparisons) and that the means for roots from the serpentine soils did not differ from each other (P = 0.31).

Elemental analysis of the soils used in the above experiment showed several differences between the serpentine soils and the non-serpentine soil (Table 1). Notable were the elevated Ni levels in the two serpentine soils, along with the lower Ca/Mg ratios for those soils relative to the non-serpentine soil. Also, Serpentine Soil 2 had an unusually high Ca content, giving it a higher Ca/Mg ratio than is usual for serpentine soils (Brooks 1987).

DISCUSSION

Our experiments showed that the Ni hyperaccumulator species, *S. polygaloides,* was more Ni tolerant than either the congeneric serpentine soil species or the unadapted species. This contrast was consistent for both the germination and the root elongation experiments. This finding for *Streptanthus* is consistent with earlier work using species of *Alyssum* and *Thlaspi.* Both Morrison et al. (1980) and Kramer et al. (1996) reported greater Ni tolerance, as measured by root elongation or biomass comparisons, for Ni-hyperaccumulating *Alyssum* species relative to non-hyperaccumulators that grew on serpentine soil. Shen et al. (1997) reported greater Ni tolerance in *T. caerulescens* relative to the non-hyperaccumulating serpentine species *T. ochroleucum.* Thus, we can extend the generality of the correlation between Ni hyperaccumulation ability and enhanced Ni tolerance to yet another

genus within the Brassicaceae, in this case to include an annual hyperaccumulating species. We hope that additional tests of this hypothesis may be undertaken using congeneric taxa from another family. The recent discovery by Reeves et al. (1996; 1999) of a large number of Ni hyperaccumulators from Cuba, many within the genera *Phyllanthus* and *Leucocroton* (Euphorbiaceae) and *Buxus* (Buxaceae), provides an excellent opportunity for such research. These genera would also allow extension of these questions to include woody (shrub, tree) growth forms.

As pointed out earlier, equivalent metal tolerance between hyperaccumulator and non-hyperaccumulator species from serpentine soils would constitute evidence contrary to both the tolerance and elemental allelopathy hypotheses. However, our results, plus those reported earlier (Morrison et al. 1980; Gabbrielli et al. 1990; Homer et al. 1991; Kramer et al. 1997; Shen et al. 1997), showed greater metal tolerance by the hyperaccumulator species studied. These results are consistent with both the tolerance and the elemental allelopathy hypotheses.

More information is needed to decide whether either of these hypotheses provides an evolutionary rationale for metal hyperaccumulation. For example, the elemental allelopathy hypothesis requires that soil Ni levels under hyperaccumulating plants are significantly higher than in other microsites. If this occurs, then the lesser Ni tolerance of co-occurring plant species might put them at a competitive disadvantage relative to hyperaccumulating species. Our (and other) Ni tolerance tests indicate that elemental allelopathy may indeed provide an adaptive rationale for metal hyperaccumulation.

Unfortunately, little information on the microdistribution of soil Ni around hyperaccumulator plants is available. Two preliminary reports (Baker et al. 1992; Schlegel et al. 1992) indicated that localized Ni enrichment might occur. A third study (Boyd and Jaffré in review) also documented significantly greater surface soil Ni concentrations under canopies of the Ni-hyperaccumulating tree, *Sebertia acuminata* Pierre *ex* Baillon, compared to surface soil under the canopies of nearby non-hyperaccumulator tree species. In contrast, a study by Boyd et al. (1999), using the New Caledonian Ni hyperaccumulating shrub *Psychotria douarrei* (Beauvis.) Daniker, provided information contrary to this hypothesis. They analyzed soil Ni content under shrubs ranging in size from saplings to full-sized adults. No correlation of soil Ni with shrub size was detected, indicating that Ni enrichment was not occurring in that case.

We also point out that enhanced tolerance of soil metals by hyperaccumulators may result in another ecological advantage apart from the elemental allelopathy hypothesis discussed above. Greater metal tolerance would allow hyperaccumulators to exploit relatively high-metal soil microsites that might

exist on serpentine sites. If other serpentine soil species are unable to grow (or are unable to grow well) in these microsites, hyperaccumulators might avoid competition for soil water/nutrients and thus gain a survival advantage. We call this the "microsite tolerance" hypothesis, to separate it from the elemental allelopathy hypothesis discussed previously.

Even for an annual species like *S. polygaloides,* enhanced Ni tolerance could allow colonization of relatively high-Ni microsites that are not exploited by other species, resulting in a survival advantage. The variability of metal levels within and between serpentine soil sites has been noted before (Kruckeberg 1984), including recent studies on serpentine soils from California (Nicks and Chambers 1998). Field investigations of the relationship between *S. polygaloides* density and soil Ni levels would provide evidence pertinent to this hypothesis, but to our knowledge such studies have not been conducted. We should note that the microsite tolerance function of hyperaccumulation might intergrade with elemental allelopathy. For example, seedlings of a metal hyperaccumulator that become established on a microsite containing elevated soil metals might, over time, further elevate surface soil metal content and thus extend the boundaries of the high-metal microsite. The concentration of metals into surface soil, along with the expanded area of the microsite, could then provide a survival advantage via elemental allelopathy.

The tolerance hypothesis is more difficult to completely falsify. Hyperaccumulators must, by definition, possess the ability to tolerate high tissue metal levels. Therefore, demonstration of greater Ni tolerance by hyperaccumulators does not contradict this hypothesis but does not provide definitive evidence that tolerance is an adaptive function of hyperaccumulation. Our experimental result, demonstrating greater Ni tolerance of *S. polygaloides* relative to *S. breweri,* is consistent with the tolerance hypothesis. However, several authors have suggested that tolerance and hyperaccumulation are not strongly linked traits. Ingrouille and Smirnoff (1986) first suggested this for *Thlaspi caerulescens,* stating that Zn tolerance and Zn hyperaccumulation in that species may be independently inherited. Meerts and Van Isacker (1997) compared Zn hyperaccumulation and tolerance among populations of *Thlaspi caerulescens* collected from high- and low-metal soil sites. They found that the low-metal populations were able to hyperaccumulate Zn to a greater extent, but the high-metal populations were more Zn tolerant.

We suggest that other approaches can more clearly address this question. Perhaps the creation of non-hyperaccumulating mutants of a metal hyperaccumulator species, that can then be used to compare metal tolerances, can provide another way to test this hypothesis. Until that point, the tolerance hypothesis must be regarded as a possibly viable

explanation for the adaptive value of metal hyper-accumulation.

Our soil-based experiment showed that solution-based root elongation tests may mirror the effects of Ni in soils, but suggested that factors other than Ni content may affect root elongation in serpentine soils. That *Brassica* root elongation was less in serpentine soils was not surprising, as this species does not possess adaptations that allow it to tolerate serpentine soil conditions. The result of the soil-based experiment with *S. polygaloides* (greater elongation in serpentine soils) was unexpected. One explanation for this result might be that *S. polygaloides* requires elevated soil Ni for optimum root growth. A higher metal requirement for hyperaccumulators has been suggested by some experiments (e.g., Shen et al. 1997) but not others (e.g., Morrison et al. 1980, Kramer et al. 1996). Results of our root elongation experiment do not show a Ni^{+2} requirement for *S. polygaloides,* as all species we tested showed a decline in root elongation at the lowest Ni^{+2} level tested (0.085 mmol/L) relative to the control solution. In contrast, Nicks and Chambers (1995) reported lower biomass for *S. polygaloides* individuals grown in very low-Ni^{+2} nutrient solutions, and suggested that some level of Ni^{+2} in the growth medium was needed for optimum growth. We have noted mixed results in our own studies with *Streptanthus polygaloides.* In one experiment (Martens and Boyd 1994), plants grown on high-Ni greenhouse soil had less biomass than plants grown on low-Ni greenhouse soil. A second experiment (Boyd et al. 1994) showed the opposite result.

A second explanation may involve interactions between a hyperaccumulator and the soil microflora. For *S. polygaloides,* this could be a positive (in the serpentine soil) or a negative (in the non-serpentine soil) interaction that could produce the difference in root growth that we observed. Soil pathogens have been reported to limit plant growth when serpentine soil species are grown in low-Ni soil. For example, Tadros (1957) reported that soil-borne pathogens caused damping-off of seedlings of a serpentine soil non-hyperaccumulator *Emmenanthe* species when seedlings were grown on non-serpentine soil. Also, Brooks (1987) reported that Ni hyperaccumulators in the genus *Alyssum* could be difficult to grow on low-Ni soil due to apparent pathogen attack. Certainly, it seems likely that the performance of serpentine soil species on their native soils will be affected by similar organismal interactions, and that these interactions might be affected by the elevated metal contents of hyperaccumulators. The possible consequences of these hyperaccumulator/soil microflora interactions are only now being articulated (e.g., Boyd and Martens 1998).

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ANNUAL VARIATION IN XYLEM WATER POTENTIAL IN CALIFORNIA OAKS

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Abstract

We measured late-summer predawn, daytime and the overnight recovery of xylem water potential for six years in *Quercus lobata* Nee, *Q. douglasii* Hook. & Arn. and *Q. agrifolia* Nee. Predawn xylem water potential was positively correlated with the rainfall in the previous year, indicating that low rainfall years are experienced as dry years by these oaks. *Quercus douglasii* had consistently lower xylem water potential than the other two species. Predawn values were consistently different among individuals trees and species, but the daytime and recovery values converged in the wet years. These results indicate that one-time measurements of predawn xylem water potential are a good indicator of species and individual tree differences in access to soil moisture.

The pressure bomb technique is an easy, reliable method of measuring xylem water potential of trees in the field (Koide et al. 1991; Ritchie and Hinckley 1975; Turner 1981) and is widely used as an indication of water stress of individuals (Callaway et al. 1991; DeLucia et al. 1988; Donovan and Ehleringer 1994; Knops and Koenig 1994; Kolb and Davis 1994; Stringer et al. 1989). Implicit assumptions of these studies are that inter-annual variation in environmental conditions have a minimal effect on either the ranking of individuals or species-specific water stress such that differences in water stress are consistent from year to year. We tested this assumption in three species or California oaks by measuring xylem water potential in the same trees in six different years.

Based on the large number of trees measured during the first year of the study, we previously reported differences among the species: *Quercus douglasii* Hook. & Arn. (blue oak), a winter deciduous species, exhibited low xylem water potential values, indicative of little access to ground water; *Q. lobata* Nee (valley oak), a second winter deciduous species, exhibited significantly higher values indicating good access to ground water; and *Q. agrifolia* Nee (coast live oak), an evergreen species with high daytime and predawn xylem water potential values, indicating limited transpiration during the dry part of the year (Knops and Koenig 1994).

Methods

This study was conducted at the Hastings Natural History Reservation in central coastal California. The landscape consists of a mosaic of Mediterranean grasslands, oak woodlands, chaparral and riparian areas (Griffin 1988; Knops et al. 1995). Rainfall was measured daily and we used the annual total from September 1 of the previous year through August 30 of the current year.

We measured xylem water potential of 14 *Q. agrifolia,* 13 *Q. douglasii* and 13 *Q. lobata* trees. These trees were selected from 250 trees of five species that are part of a long-term study examining acorn productivity (Knops and Koenig 1994, 1997; Koenig et al. 1994, 1996). Trees were selected to represent a gradient in acorn productivity within each species and are located throughout Hastings over a distance of approximately 3.5 km.

Xylem water potential was measured using a pressure bomb (PMS Instruments Co.) in September of each year, the end of the dry season when temperatures are hottest and water stress the greatest (Knops and Koenig 1994). Daytime measurement were made between 1300 and 1700, whereas predawn measurements on the same trees were made on the subsequent night between 0200 and 0600. Recovery was calculated as daytime minus predawn. Shoots with a minimum of three leaves and approximately 5 cm long were cut and immediately measured in the field. Shoots were not bagged, because we found no differences with samples pre-bagged in plastic. All daytime shoots were cut in direct sunlight. We measured 2 shoots per tree, except if the values were more than 10% different, in which case we measured a third shoot. Measurements were taken in 1991 and 1994 through 1998. In each year trees were measured at the end of the dry season in September.

Results

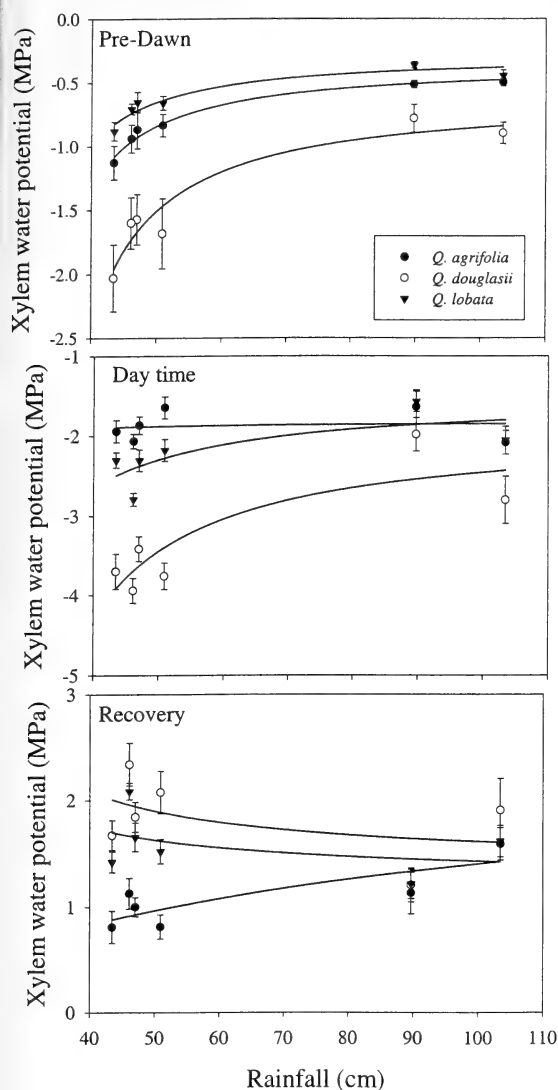There was a significant positive relationship between the amount of rainfall and the predawn xy-

FIG. 1.   Predawn, daytime and recovery (calculated as daytime - predawn) xylem water potential of *Q. lobata* (n = 14), *Q. douglasii* (n = 13) and *Q. agrifolia* (n = 13). Given are the means ±1 S.E. for the years (from left to right) 1994, 1996, 1991, 1997, 1995, 1998. Predawn xylem water potential, *Q. agrifolia* F = 184, R^2 = 0.98, P < 0.001; *Q. douglasii* F = 45, R^2 = 0.92, P < 0.003; *Q. lobata* F = 47, R^2 = 0.92, P < 0.003; midday xylem water potential *Q. douglasii* F = 11, R^2 = 0.73, P < 0.03; all other regressions are P > 0.05.

lem water potential of all three species, but there was a significant relationship between daytime xylem water potential and rainfall only in *Q. douglasii* (Fig. 1). None of the species exhibited a significant relationship between the overnight recovery and rainfall (Fig. 1).

Although all three xylem water potential measurements were significantly concordant among the individual trees over the six-years of the study, predawn values were consistently more similar from

year to year than either of the other measures (Kendall's coefficient of concordance, predawn 0.653, day 0.298, recovery 0.184, all Chi-Square >39, all P < 0.000).

Quercus douglasii and *Q. agrifolia* had consistently lower predawn xylem water potential values than *Q. lobata* (one way ANOVA with Scheffe's post hoc comparison; *Q. douglasii* P < 0.05 in all 6 years; *Q. agrifolia* P < 0.05 in all years, except 1995). *Q. douglasii* had consistently the lowest daytime values (significant from *Q. lobata* in 4 out of 6 years, not in 1995 and 1998), with *Q. lobata* having intermediate values (significantly different from *Q. agrifolia* 2 out of 6 years, e.g., 1996 and 1997). Recovery was greater for *Q. douglasii* and *Q. lobata* than for *Q. agrifolia* (significant 4 out of 6 years, not in 1995 and 1998).

DISCUSSION

Does xylem water potential reflect rainfall? Predawn xylem water potential values were significantly correlated with rainfall in all three species. This supports the assumption that predawn xylem water potential measured in the driest period of the year reflects relative water availability and that these oak species experience lower water status in dry years. Predawn values were consistently significantly different among the species, and the differences were largest in drier years. In contrast, daytime and recovery xylem water potential values converge in wet years (Fig. 1) and have only a limited value in characterizing differences among species.

Are individuals and species different over time? Measurements for individual trees were significantly concordant from year to year, more so for predawn than daytime or recovery values. Thus, predawn xylem water potential apparently reflects real and consistent differences among individuals in either their access to water, in their genetic ability to acquire water or in their ability to conserve water.

Our data also support the hypothesis that predawn xylem water potential values are consistently significantly different among the species, with *Q. douglasii* being more water stress tolerant, because of its low predawn xylem water potential and the significant relationship between rainfall and daytime xylem water potential. However, this scenario does not fit the other two species. These differences are consistent with the limited data on root distribution of these three species. *Quercus lobata* is reported as having a deep root system connected to the ground water (Griffin 1973), which might make it less sensitive to the previous 12 months rainfall and more sensitive to long term changes in ground water levels. *Quercus agrifolia* has an extensive shallow system (Canon 1914a, 1914b) and presumably lacks access to the previous winter precipitation, which is likely stored in deeper soil levels and *Q. douglasii,* which does not have consistent access

to groundwater (Griffin 1973). This also raises the alternative hypothesis that these oak species might differ in critical water potential for cavitation (e.g., the formation of unreversible air bubbles within the xylem vessels). Cavitation can be a significant cause of hydraulic conductivity loss within oaks due to water stress (Tognetti et al. 1996, 1998) and species specific differences in vulnerability of cavitation have been reported for oak species (Cocard et al. 1996; Tognetti et al. 1996). Lastly, differences in water conservation caused by differences in phenology and physiology among the species may also have contributed to these patterns.

The lack of a relationship for *Q. agrifolia* and *Q. lobata* correlation between midday xylem water potential and the rainfall and the lack between recovery and rainfall for all three species indicates that the degree to which xylem water potential recovers overnight is not dependent on rainfall. Instead, individual trees may be able to lower their predawn xylem water potential, and in the case of *Q. douglasii* daytime xylem water potential, thereby increasing water uptake in the driest years. This does not imply that the activity of the trees is the same in each year, as the time that the stomates are open in the daytime might be correlated with the amount of water available for transpiration. Alternatively, this might also indicate a strict regulation for water loss for *Q. agrifolia* and *Q. lobata,* via stomatal conductance or adjustment in hydraulic conductance to avoid cavitation and *Q. douglasii* might have a lower critical threshold for cavitation. Testing this would require measuring daily patterns of xylem water potential, hydraulic conductivity and cavitation, which we did not do as part of this study.

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MOLECULAR EVIDENCE FOR THE HYBRID ORIGIN OF *OPUNTIA PROLIFERA* (CACTACEAE)

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Abstract

Opuntia prolifera Engelm., (Coastal Cholla) is common to the coastal sage scrub community extending from Ventura County, California to El Rosario, Baja California. On the basis of morphological intermediacy, *O. prolifera* is suspected to have originated through hybridization between *O. alcahes* and *O. cholla,* both species of coastal and inland deserts of Baja California and Baja California Sur. For an independent test of this hypothesis, we generated RAPD banding patterns from exemplars of different populations of *O. prolifera* and the putative parents. In order to exclude other potential parents and to distinguish species-specific RAPD bands we included *O. bigelovii* Engelm., *O. ganderi, O. tesajo,* and *O. wolfii* (L. Benson) M. Baker in the screening. The results provide support for the hybridization hypothesis as well as some insight into the speciation process. Twenty-nine primers revealed 44 bands shared only between *O. prolifera* and one or the other putative parent. No other species included in the screening proved to be comparable alternatives to *O. alcahes* or *O. cholla* as the parents of *O. prolifera.* Unique bands are rare (=2) in *O. prolifera* compared with *O. alcahes* (=19) and *O. cholla* (=23). Trends in the degree of band sharing between *O. prolifera* and representatives of *O. alcahes* and *O. cholla* suggest a central Baja California origin of the species.

The dynamic geologic and climatic history of Baja California has fostered a diverse and highly endemic flora on the peninsula, and one of the most speciose genera is *Opuntia* (Cactaceae). The speciation routes taken by *Opuntia* have also been diverse: many species are proven hybrids and many more exhibit multiple ploidal levels (D. Pinkava pers. comm.). One suspected hybrid, *Opuntia prolifera* Engelm., was until recently considered a species derived through cladogenesis.

Opuntia prolifera (Coastal Cholla) occurs in the coastal sage scrub community adjacent to the Pacific Ocean between Cedros Island, Baja California and Ventura County, California. This taxon is triploid (Pinkava et al. 1992) and reproduces almost exclusively asexually, usually through dispersal of detached stem segments. Morphological intermediacy of *O. prolifera* between *O. alcahes* F. A. C. Weber and *O. cholla* F. A. C. Weber in several characteristics (Table 1) has prompted speculation that *O. prolifera* may have arisen through hybridization of these species (Rebman 1995). *Opuntia alcahes* and *O. cholla* are desert taxa of Baja California and typically diploid (Pinkava et al. 1992; Rebman 1995). The two species commonly grow sympatrically without hybridizing (Fig. 1), however a hybrid swarm involving the two species exists near El Rosario (Rebman 1995)—which is in the southern part of the range of *O. prolifera,* an area of overlap between the Sonoran Desert and the California Floristic Province (Fig. 1). Despite the general intermediacy of *O. prolifera,* phenotypic plasticity of the putative hybrid and parent species prevents a strong case for hybridization to rest on morphological data alone.

To subject the hybridization hypothesis to further scrutiny, we surveyed patterns of Random Amplified Polymorphic DNA (RAPD) markers obtained from *O. prolifera* and its putative parents. The RAPD technique allows relatively quick assessment of a large number of highly polymorphic loci, largely of the nuclear genome (Welsh and McClelland 1990; Williams et al. 1990). Recent studies have successfully applied the RAPD approach to questions of interspecific hybridization (Pham and Smith 1995; Barker et al. 1996; Daehler and Strong 1997) and hybrid speciation (Smith et al. 1995; Lifante and Aguinagalde 1996; Allan et al. 1997; Padgett et al. 1998).

We used RAPD data to test if *Opuntia prolifera* exhibits the classic genetic expectations of hybrid taxa. If the putative parent species, *O. alcahes* and *O. cholla,* were sufficiently divergent genetically prior to a hybridization event, then the hybrid, i.e., *O. prolifera,* should exhibit additivity of genetic markers specific to the parent species as well as a lack of unique markers (Gallez and Gottlieb 1982). Additionally, the sterile triploid nature of *O. prolifera* suggests the possibility that "fixed" heterozygosity (***sensu*** Roose and Gottlieb 1976) in *O.*

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TABLE 1. SELECTED MORPHOLOGICAL CHARACTERISTICS OF *OPUNTIA PROLIFERA* AND ITS HYPOTHESIZED PARENTS, *O. ALCAHES* AND *O. CHOLLA,* IN REGIONS OF SYMPATRY (FROM REBMAN 1995).

Characteristic	*O. alcahes*	*O. prolifera*	*O. cholla*
Inner tepal color	yellow, green, or red-magenta	magenta to deep red	light to dark pink
Stem segment shape	long and narrow (3.5–13 × 1.5–4.5 cm)	intermediate (7.5–12.6 × 3.0–4.1 cm)	short and wide (6–11.5 × 3–5.5 cm)
Tubercule length	4–22 mm	12–24 mm	20–35 mm
Tubercule height	2–9 mm	5–9 mm	10–20 mm
Spine shape	short and thin (4–20 × 0.3–0.5 mm)	intermediate (14–18 × 0.7–0.9 mm)	long and thick (20–35 × 0.8–1.3 mm)
Areole size	3–5 × 2–4 mm	5–8 × 3–5 mm	6–11 × 3–5 mm
Proliferating fruit	rare	yes	yes

prolifera could endow it with a higher overall number of RAPD markers relative to its putative parents. Finally, patterns in the degree of band sharing between hybrid and parents can also be used to make preliminary inferences regarding the geographic region in which the hybrid taxon arose, as well as the possibility that this event occurred multiple times.

METHODS

Field collection and DNA extraction. Stem segments were gathered from a single plant (exemplar) at each location (Table 2). DNA was extracted from fresh or frozen stem tissue following a modification (Doyle and Doyle 1987) of the hot CTAB method of Saghai-Maroof et al. (1984).

Initial RAPD screening. DNA extracts from *Opuntia alcahes, O. prolifera,* and *O. cholla* were subjected to DNA amplification via the polymerase chain reaction (PCR) using the 100 10-mer primers of RAPD Oligo Set 3 (Nucleic Acid-Protein Service Unit of the University of British Columbia). Each 25 µL reaction contained 1 unit of Promega (Madison, WI) *Taq* polymerase, 1× reaction buffer,

TABLE 2. COLLECTIONS OF *OPUNTIA* FROM CALIFORNIA AND MEXICO ANALYZED IN THE PRESENT STUDY; PRECISE LAT./LONG. DATA ARE AVAILABLE UPON REQUEST. Exemplars are given abbreviated names for reference in text, tables, and figures; B.C. = Baja California, B.C.S. = Baja California Sur; asterisk denotes collections used in initial screening only.

| Species	Collection	Location
O. alcahes F. A. C. Weber		
	Rebman s.n.*	CA., San Diego Co., Quail Botanical Gardens
alc 1	Voss 1174	B.C.S., Cape Region
alc 2	Rebman 4157	B.C., southwest of Cataviña
alc 3	Rebman 4835	B.C.S. near Rt. 1 and rd. to Punta Abreojos
alc 4	Rebman 5183	B.C. Sur, Sierra Guadalupe
O. bigelovii Engelmann var. *Bigelovii*	Rebman 4956	CA., San Diego Co., Hwy S-2 at Canebrake
O. cholla F. A. C. Weber		
cho 1	Rebman 4158	B.C., southwest of Cataviña
cho 2	Rebman 4501	B.C.S., Sierra San Francisco
cho 3	Rebman 4827	B.C.S., Isla Margarita
cho 4	Rebman 5184	B.C.S., Sierra Guadalupe
O. ganderi (C. B. Wolf) J. Rebman & D. J. Pinkava	Rebman 4973	B.C., San Felipe Desert, n. of Laguna Diablo
O. prolifera Engelmann		
pro 1	Mayer 591	CA., San Diego Co., U.S.D. campus, West Point
pro 2	Rebman 3951	B.C., between La Bocana and Puerto Santo Tomás
pro 3	Rebman 3977	B.C., s. of Punto Canoas
pro 4	Rebman 5119	B.C., near La Mision
O. tesajo Engelmann	Rebman 4972	B.C., San Felipe Desert, n. of Laguna Diablo
O. wolfii (L. D. Benson) M. A. Baker	Rebman 3820	CA., Imperial Co., along I-8 at Mountain Springs Grade
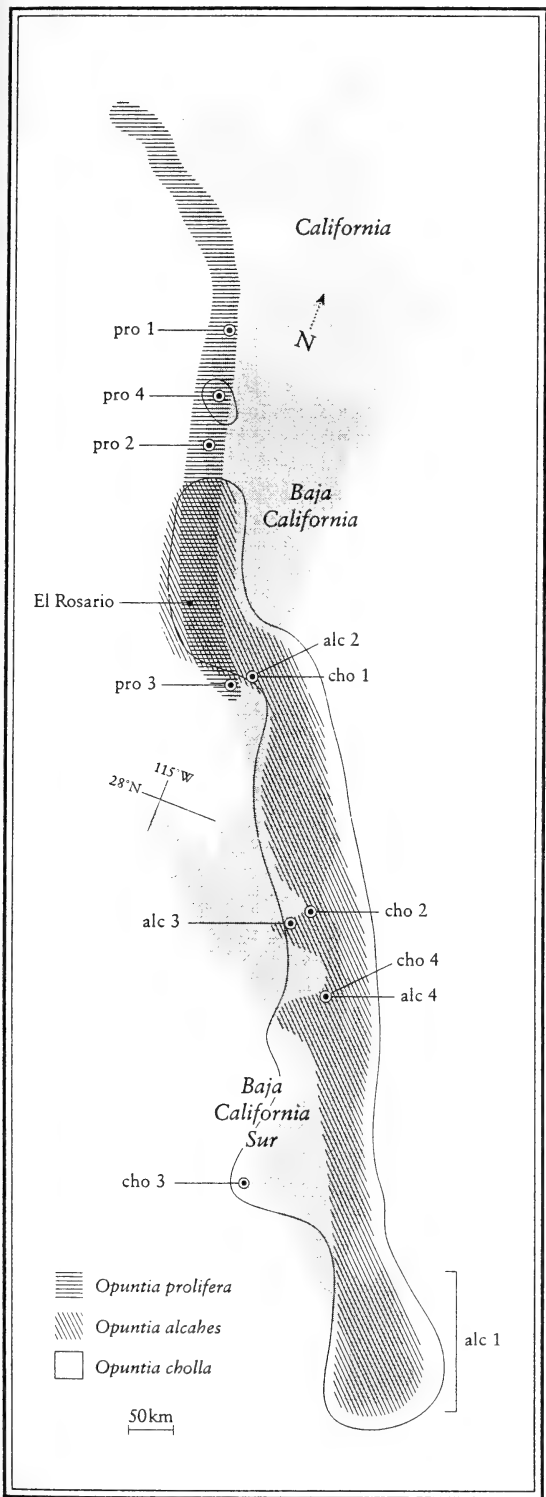
Fig. 1. Ranges of *Opuntia prolifera*, *O. alcahes*, and *O. cholla*; locations of collections used for population-level comparisons are noted by abbreviated names listed in Table 2.

1.5 mM $MgCl_2$, 0.1 mM of each dNTP, 0.2 µM of one primer, and 1 µl dilute DNA extract. After 2 min at 94°C, the following cycle was repeated 40 times: denaturing at 94°C for 15 s, annealing at 36°C for 1 min, and elongation at 72°C for 1 min. A final elongation segment was held at 72°C for an additional 6 min. The PCR products were separated electrophoretically in 2% agarose gels and banding patterns were visualized by staining with ethidium bromide and inspection under ultraviolet light. Of the 100 primers, twenty-one showed banding polymorphism and the sharing of bands between exemplars of *O. prolifera* and either *O. alcahes* or *O. cholla*; therefore these primers were used in subsequent screening experiments.

To replicate the patterns observed in the first round of screening and to identify bands shared between *O. prolifera* and only *O. alcahes* or *O. cholla*, we included other related species (*O. bigelovii*, *O. ganderi*, *O. tesajo*) in new screening experiments using the primers identified in the first round. We assumed that any marker that was also present in one of these additional species was a symplesiomorphic characteristic and not helpful in a rigorous test of the hybridization hypothesis. *Opuntia prolifera* exhibited a total of five bands that it shared only with both the putative parents, six bands that it shared only with *O. alcahes,* and eight bands that it shared only with *O. cholla.* When *O. prolifera* was compared in the same way with *O. bigelovii*, *O. ganderi*, and *O. tesajo,* the numbers of exclusively-shared markers were zero, two, and one, respectively.

Primary RAPD screening. The results of the initial rounds of screening increased our confidence that *Opuntia prolifera* was a hybrid derivative of *O. alcahes* and *O. cholla.* We then examined the distribution of RAPD markers among populations within these species. We employed the same primers that had proven useful in previous rounds of screening and increased our sample sizes of *O. prolifera, O. alcahes,* and *O. cholla* to include an exemplar from four populations of each taxon (Table 2). In addition, one exemplar each was included from *O. bigelovii, O. ganderi, O. tesajo,* and *O. wolfii.* This allowed us to (1) replicate previously observed patterns and identify additional bands shared only between the putative hybrid and its parents, (2) get a cursory look at intraspecific RAPD polymorphism, and (3) assess the degree of band sharing on a pairwise population level and, subsequently, compare these data to the geographic distribution of the populations represented.

RESULTS

Banding patterns derived from screening 16 exemplars using 29 RAPD primers revealed a greater number of markers in support of the hybridization hypothesis than did the initial comparisons (Table 3), presumably because more of the total variation

TABLE 3. PRIMERS THAT RESOLVE MARKERS SHARED EXCLUSIVELY BETWEEN *OPUNTIA PROLIFERA* AND ITS PUTATIVE PARENTS. A = *O. alcahes*, C = *O. cholla*, A+C = both species.

Primer	Sequence	Markers shared with *O. prolifera*		
		A	C	A+C
UBC 202	GAGCACTTAC	2	0	0
UBC 204	TTCGGGCCGT	1	0	0
UBC 218	CTCAGCCCAG	1	0	0
UBC 219	GTGACCTCAG	1	1	2
UBC 220	GTCGATGTCG	3	1	0
UBC 225	CGACTCACAG	1	2	1
UBC 226	GGGCCTCTAT	1	2	0
UBC 227	CTAGAGGTCC	0	1	0
UBC 228	GCTGGGCCGA	1	1	0
UBC 238	CTGTCCAGCA	0	1	0
UBC 245	CGCGTGCCAG	1	0	0
UBC 246	TATGGTCCGG	1	1	0
UBC 247	TACCGACGGA	0	2	0
UBC 250	CGACAGTCCC	0	1	1
UBC 253	CCGTGCAGTA	1	2	0
UBC 259	GGTACGTACT	2	1	0
UBC 260	TCTCAGCTAC	1	0	0
UBC 269	CCAGTTCGCC	1	2	0
UBC 270	TGCGCGCGGG	1	2	0
UBC 275	CCGGGCAAGC	0	1	0
UBC 281	GAGAGTGGAA	3	0	1
UBC 283	CGGCCACCGT	1	0	0

TABLE 4. SUMMARY DATA FROM PRIMARY SCREENING OF RAPD PATTERNS IN *OPUNTIA PROLIFERA* (P) AND ITS PUTATIVE PARENTS *O. ALCAHES* (A) AND *O. CHOLLA* (C).

Characteristic	P	A	C
Total bands examined	167	164	164
Unique bands	2	19	23
Bands shared only with P	—	23	21
Bands shared only with P, fixed for both taxa	—	3	5
Bands shared only between A and C	—	1	
Bands shared only among A, C, and P		5	

the RAPD data provided the means to assess overall similarity among the exemplars included in the study. The first two factors account for 41.5% and 16.8% of the variance in the data set. Plotting the exemplars by their scores along factors one and two places *O. prolifera* clearly intermediate between *O. alcahes* and *O. cholla* (Fig. 2).

Estimates of banding pattern similarity between pairs of populations of *O. prolifera* and *O. alcahes* or *O. cholla* were made in two ways: using the Simple Matching Coefficient (Sokal and Michener 1958) and the Coefficient of Jaccard (Sneath 1957). We tallied presence or absence of marker bands for all pairwise comparisons of exemplars of *O. prolifera* vs. *O. alcahes* or *O. cholla*. We ignored bands that were fixed for all exemplars of the two taxa being compared in an effort to minimize the effect of symplesiomorphies on the coefficient. The Simple Matching Coefficient (SMC) was calculated by adding the matches (shared absences plus shared presences of markers) and dividing by the total number of matches and mismatches. The Coefficient of Jaccard (CJ) omits shared absences from the numerator and denominator. We were concerned that the SMC would be biased by artefacts

within each species was assessed and more primers were successful. Pairwise comparisons between exemplars of *O. prolifera* and *O. alcahes,* or *O. prolifera* and *O. cholla* revealed 23 and 21 bands, respectively, present in at least one population of the two species compared, and found in no other species (Tables 3, 4). Of these 44 marker loci, the group of *O. prolifera* exemplars is polymorphic for at least 31 (>70%). A comparison between *O. alcahes* and *O. cholla* detected just one shared band, which was unique to just one exemplar of each species. A comparison of *O. prolifera* exemplars against representatives of *O. bigelovii, O. ganderi, O. tesajo,* and *O. wolfii* revealed one, one, zero, and zero bands, respectively, that were exclusively shared. Of the aforementioned markers of hybridization, only a small number are fixed in all exemplars of *O. prolifera* and *O. alcahes* (=3) or *O. prolifera* and *O. cholla* (=5) (Table 4). Five additional bands were shared exclusively among *O. prolifera* and both putative parents.

Opuntia prolifera did not possess a significantly greater number of bands (P = 0.97) compared with its putative parents: 167 bands total versus 164 in both *O. alcahes* and *O. cholla* (Table 4). Comparison of *O. prolifera* with its putative parents also revealed significantly (P < 0.01) fewer unique bands in *O. prolifera* (n = 2) than in either *O. alcahes* (n = 19) or *O. cholla* (n = 23) (Table 4). A factor analysis (Statview 5.0, SAS Institute, Inc. 1998) of
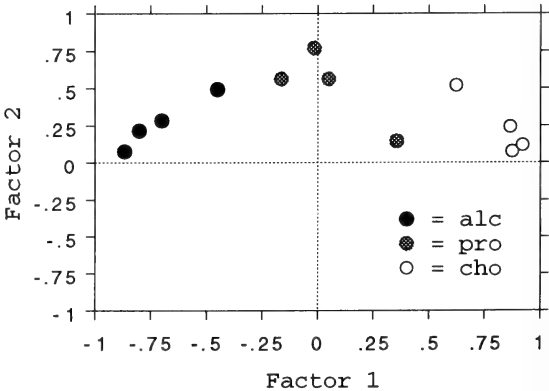

FIG. 2. Unrotated factor plot showing position of exemplars along factors one and two; refer to Table 2 for key to abbreviations.

TABLE 5. PAIRWISE SIMILARITY COEFFICIENTS BETWEEN EXEMPLARS MEASURING *OPUNTIA PROLIFERA* (PRO) × *O. ALCAHES* (ALC) AND *O. PROLIFERA* × *O. CHOLLA* (CHO). Simple Matching Coefficients before slash, Coefficient of Jaccard after; see Table 2 for key to abbreviations.

	pro 1	pro 2	pro 3	pro 4
alc 1	0.539/0.143	0.524/0.231	0.359/0.242	0.225/0.184
alc 2	0.583/0.000	0.568/0.111	0.250/0.069	0.189/0.063
alc 3	0.475/0.160	0.512/0.259	0.525/0.424	0.342/0.308
alc 4	0.436/0.154	0.475/0.250	0.539/0.455	0.400/0.368
cho 1	0.528/0.150	0.421/0.120	0.297/0.212	0.447/0.364
cho 2	0.650/0.263	0.600/0.200	0.263/0.125	0.250/0.167
cho 3	0.528/0.105	0.526/0.182	0.243/0.152	0.368/0.273
cho 4	0.514/0.182	0.462/0.192	0.324/0.242	0.487/0.412

arising from poor amplification, thereby inflating estimates of similarity between two populations. As expected, the SMC values were uniformly greater than the CJ values (Table 5), but in some cases the two approaches yield different patterns of relationships among the populations. For example, the two sets of coefficients comparing pro 2 with the four populations of *O. alcahes* display almost opposite rankings by magnitude (Table 5), perhaps indicating that the inclusion of shared absences does indeed bias the SMC in this application.

Considering, therefore, only the CJ values we see that among all the exemplars of *O. alcahes* and *O. cholla,* two exemplars of *O. prolifera* (pro 1 and 2) exhibited greater similarity, albeit by narrow margins, to alc 3 and cho 2 (Table 5). In contrast, pro 3 and pro 4 exhibited greater similarity to alc 4 and cho 4. These relationships also had geographic significance: exemplars alc 4 and cho 4 were collected from the same vicinity in northern Baja California Sur, and alc 3 and cho 2 were collected just 40 km apart, also in northern Baja California Sur (Fig. 1).

DISCUSSION

Molecular evidence supports the proposition that hybridization between *Opuntia alcahes* and *O. cholla* gave rise to *O. prolifera.* Forty-four RAPD markers are shared only between *O. prolifera* and one or the other parent species; no other candidates emerge as comparable alternatives to *O. alcahes* or *O. cholla* as the parents of *O. prolifera.* As expected for a hybrid, *O. prolifera* exhibits significantly fewer unique RAPD markers than its parent species. Moreover, multivariate analysis of marker distribution places exemplars of *O. prolifera* intermediate between those of *O. alcahes* and *O. cholla.*

Some results of this study, however, were contrary to early expectations. First, *O. prolifera* banding patterns did not exhibit the greater numbers of loci predicted for a sterile hybrid or allopolyploid (Table 4). This observation may indicate a relatively low degree of divergence between *O. alcahes* and *O. cholla,* or a low amount of variation derived from the actual hybridization event, or it may expose a limitation of RAPD markers in this appli-

cation: RAPDs are dominant, diallelic markers and thus may not show the same patterns of additivity as codominant markers. Another surprising outcome was the RAPD polymorphism evident among exemplars of *O. prolifera,* indicating interpopulational genetic diversity. Because *O. prolifera* is only known to reproduce asexually, this variation may signify one or more of the following: (1) multiple independent hybrid origins of *O. prolifera,* (2) undetected sexual reproduction, or (3) genetic divergence via somatic mutations. We introduce these alternative processes briefly below, but leave a critical analysis to future studies specifically targeted to discriminating among these phenomena.

First, recurrent origin of a triploid *O. prolifera* would require either that multiple diploid-level hybridizations must each have been followed by the production of triploid offspring, or that a pairing of a diploid parent with a tetraploid parent must have occurred multiple times. Because both *Opuntia alcahes* and *O. cholla* are diploid with rare exception (Rebman 1995), the latter scenario seems unlikely. If the former scenario occurred, diploid hybrids should be common and widespread in the zone of sympatry. However, only one diploid count has been documented for *O. prolifera* (Pinkava and Parfitt 1982). Despite the apparent obstacles to recurring origins of *O. prolifera,* RAPD-based relationships among exemplars employed in the present study provide some evidence in its support. Two exemplars of *O. prolifera* (pro 1 and 2) are more closely related to alc 3 and cho 2 than to the other representatives of *O. alcahes* and *O. cholla.* In contrast, the other two exemplars of *O. prolifera* (pro 3 and 4) are more closely related to alc 4 and cho 4. Furthermore, specimens alc 4 and cho 4 were collected from the same vicinity, and the locations of alc 3 and cho 2 were separated by just 40 km.

Next, for sexual reproduction to be the source of interpopulational variation, triploid *O. prolifera* plants must give rise to triploid offspring. If meiosis could occasionally generate viable gametes of varying ploidy in *O. prolifera,* we should expect more ploidal levels than just triploid in these populations. Currently, only a hybrid swarm of the El Rosario

area (Fig. 1) has yielded counts in *O. prolifera* that exceed triploidy, including a hexaploid—presumably an autopolyploid that formed through the fusion of two unreduced gametes (Rebman 1995).

Lastly, reproduction in *O. prolifera* relies perhaps exclusively on establishment of detached stem segments (Rebman 1995). Long-term clonal growth allows for the possibility that somatic mutations in branch primordia could generate RAPD variation among populations of *O. prolifera.* The importance of somatic mutations in clonal species has long been suspected and is gaining more experimental support (Ellstrand and Roose 1987, reviewed in de Kroon and van Groenendael 1997).

Origin of Opuntia prolifera. Although it is almost uniformly triploid across its range, *O. prolifera* could have originated as a diploid, through hybridization of diploid *O. alcahes* and *O. cholla.* Meiotic irregularities in this diploid hybrid allowed the production and subsequent fusion of a reduced and unreduced gamete, generating a triploid offspring. This route from diploidy to triploidy has been seen repeatedly among cactus species (D. Pinkava pers. comm.). A notable example is *O. bigelovii,* a close relative of *O. prolifera,* which apparently arose as a diploid but is now predominantly triploid (D. Pinkava pers. comm.). If indeed *O. prolifera* originated in this way, some set of factors then allowed the triploid to surpass its diploid progenitor and thrive in the coastal sage scrub of the Californias, a habitat to which few other chollas are well-adapted.

All exemplars of *O. prolifera* showed the greatest similarity to representatives of *O. alcahes* (alc 3 and 4) and *O. cholla* (cho 2 and 4) collected from the northern end of Baja California Sur, indicating a possible region of origin of *O. prolifera.* Surprisingly, this region is greatly disjunct from the present range of *O. prolifera* (Fig. 1). However, the repeated shifts in climate and vegetation in the history of Baja California cautions us from excluding this proposition prior to further investigation.

Establishment of *Opuntia alcahes* and *O. cholla* as the parents of *O. prolifera* now sets the stage for further population genetic studies, which should be aimed towards testing for recurrent origins of *O. prolifera* and the route by which it attained triploidy.

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FLORAL VARIATION IN *DELPHINIUM VARIEGATUM* (RANUNCULACEAE)

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ABSTRACT

Delphinium variegatum is subdivided into three subspecies distinguished by three floral characters. *Delphinium v. variegatum* is found in central and northern California, while *D. v. kinkiense* (an endangered taxon) and *D. v. thornei* are endemic to San Clemente Island off the coast of southern California. Broad variation is documented in most natural populations for all three floral characters. Our results indicate that the two metric characters, lateral sepal length and lower petal blade length, provide no clear distinction between the taxa. Sepal color is the least ambiguous for differentiating the subspecies, but is problematic in distinguishing between *D. v. kinkiense* and *D. v. thornei*. Sepal color exhibits a complex pattern of variation on San Clemente Island in which northern populations generally contain primarily light-flowered individuals, southern populations generally contain primarily dark-flowered individuals, and central populations may contain substantial numbers of both light- and dark-flowered individuals as well as intermediates. However, one southern population contains primarily light-flowered individuals, and almost half of the populations contain individuals having sepal colors considered to represent the two different subspecies. Further taxonomic study including additional characters is recommended to determine whether *D. v. kinkiense* and *D. v. thornei* should be considered distinct taxa.

Delphinium variegatum Torrey & A. Gray (Ranunculaceae) is a perennial larkspur that is found in grassland and open woodlands of mainland California and San Clemente Island, the southernmost of the Channel Islands off the coast of southern California (Warnock 1990b). One subspecies, *D. v.* ssp. *variegatum* (Royal larkspur), is found exclusively on the mainland and ranges approximately from northern to central California, from the coast to the Sierra Nevada ?? foothills (Fig. 1). The other two subspecies, *D. v.* ssp. *kinkiense* (Munz) M. J. Warnock (San Clemente Island larkspur; Warnock 1990a) and *D. v.* ssp. *thornei* Munz (Thorne's larkspur; Munz 1969) are insular endemics found only on San Clemente Island. The Channel Islands are thought to provide refuge for a number of species with northern affinities, including *D. variegatum* (Raven and Axelrod 1978), that once extended farther south on the mainland during Pleistocene pluvial cycles (Raven 1963).

The island endemic subspecies of *D. variegatum* are vulnerable to extinction because of their limited distribution (Skinner and Pavlik 1994). *Delphinium v. kinkiense* is listed as endangered by the U.S. Fish & Wildlife Service (USFWS) and by the California Department of Fish and Game. However, the rarest of the subspecies, *D. v. thornei*, has no special legal status, although the USFWS considers it to be a species of concern. Both of these taxa are on the California Native Plant Society List 1B (plants rare, threatened, or endangered in California and elsewhere; Skinner and Pavlik 1994).

The subspecies of *D. variegatum* are distinguished primarily by three floral characters: sepal color, lateral sepal length and lower petal blade length (Warnock 1990b, 1993, 1997; summarized in Table 1; Fig. 2). However, there is overlap among the subspecies. The mainland subspecies, *D. v. variegatum,* is differentiated from the two island subspecies by its deep royal blue flowers, as the ranges for the two metric characters encompasses the variation observed in the entire species. The two island subspecies are differentiated from each other by all three characters, in spite of considerable overlap, with *D. v. kinkiense* having mainly white, smaller flowers and *D. v. thornei* having mainly bright blue, larger flowers. Munz (1974), interestingly, had described *D. v. thornei* as having smaller flowers (sepals ca. 12 mm long) than *D. v. kinkiense* (which he recognized as a separate species, *D. kinkiense*; sepals 16–18 mm long). Current keys use sepal color to identify taxa (Warnock 1990b, 1993, 1997), although the most recent also uses density of hairs on the base of the stem to distinguish between *D. v. variegatum* and the island subspecies (Warnock 1997).

Casual observation of natural populations of *D. variegatum* on San Clemente Island suggests that hybridization may be occurring between *D. v. kinkiense* and *D. v. thornei* in some populations. At

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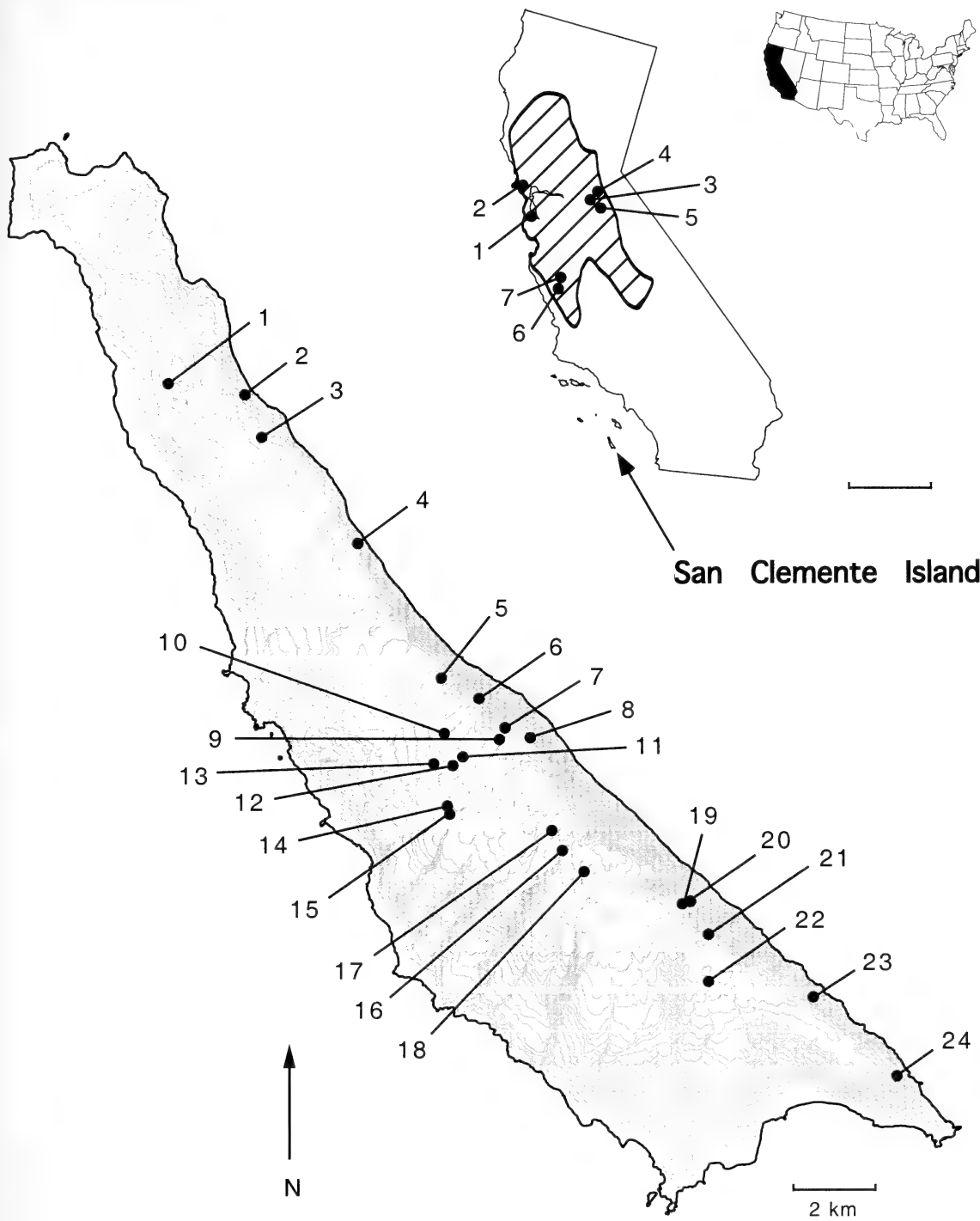
FIG. 1.   Distribution and sampled populations of *Delphinium variegatum* from mainland California (ssp. *variegatum*) and from San Clemente Island (ssp. *kinkiense* and ssp. *thornei*).

the time this study was initiated, fewer than 15 populations of *D. variegatum* were known on San Clemente Island (along with scattered individuals), with *D. v. kinkiense* occurring in the northern half of San Clemente Island and *D. v. thornei* in the southern half. However, some populations in the central part of San Clemente Island include individuals exhibiting white, bright blue or intermediate flower colors. Natural hybridization has been documented to regularly occur among other taxa in the
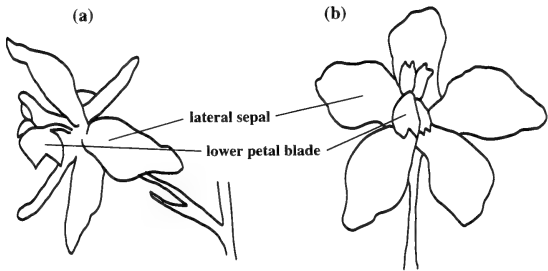
Fig. 2. Diagram of (a) side view and (b) front view of a *D. variegatum* flower.

genus *Delphinium* (Warnock 1990b, 1997); natural hybrids are known between *D. v. variegatum* and *D. hansenii, D. hesperium, D. parryi,* and *D. recurvatum* (Lewis and Epling 1954).

The goals of this study were (1) to document variation in floral morphology in natural populations of the subspecies of *D. variegatum,* (2) to evaluate the utility of the three floral characters for distinguishing *D. v. kinkiense* and *D. v. thornei,* and (3) to identify populations of *D. variegatum* on San Clemente Island as *D. v. kinkiense, D. v. thornei* or mixed populations.

Materials and Methods

Study sites. Twenty-four populations of *D. v. kinkiense* and *D. v. thornei* were located and sampled from San Clemente Island in 1996 (Fig. 1; Table 2). This represents all known populations and probably all of the populations on the island; subsequent surveys have failed to reveal additional locations (Junak and Wilken 1998; S. Burckhalter, University of South Dakota, pers. comm.; K. Helenurm, personal observation). Seven populations of *D. v. variegatum* were sampled across its range, from Marin County in the north to southern Monterey County and east to Tuolumne and Mariposa Counties. All populations of the three subspecies occurred in open grassland habitat. Island populations were found only on west or northerly aspects, probably due to moister, cooler conditions in these areas.

Flower collection and measurements. Thirty to forty-four flowering individuals were haphazardly sampled from large populations (Table 2). In smaller populations, all flowering individuals were sampled. Two flowers from each sample individual

were measured for sepal color, lateral sepal lengths, and lower petal blade lengths (Fig. 2). Sepal color was measured by matching lateral sepals to a color chart (Royal Horticultural Society 1986). Colors were quantified by matching the color chart patches to colors in Adobe Photoshop (1995) computer software using a calibrated monitor. We recorded their hue, saturation, and brightness values using the same computer system for all measurements. Values for brightness were used for analysis because brightness (quantifying the degree of lightness or darkness, ranging from 0 representing black to 100 representing white) best reflects Warnock's (1990b) descriptions of the subspecies and the range of variation in flower color we observed. Although differences in hue (the attribute of colors that permits them to be classed as blue versus lavender or purple, for example) and saturation (the degree of difference from a gray having the same lightness) occur, the quantifiable difference between white, light blue, bright blue and deep royal blue sepals is reflected in brightness values rather than hue or saturation.

In all, 775 individuals were measured for floral characters in all 24 San Clemente Island populations, and 242 individuals were measured in 7 mainland populations, for a total of 1017 individuals.

Analysis. Measurements of brightness and metric characters were averaged for different flowers of the same individual. Associations among the different floral characters in *D. v. kinkiense* and *D. v. thornei* were addressed in three ways. First, t-tests were used to test differences in lateral sepal and lower petal blade lengths in individuals with light versus dark sepal color. Second, correlations among the floral characters were tested using Pearson's correlation analysis. Third, grouping of floral characters was investigated using principal components analysis (PCA). All analyses were performed using SYSTAT (1992).

Results

Variation in floral morphology. Box plots of floral variation in *D. variegatum* illustrate broad variation in most natural populations on San Clemente Island (Fig. 3). Sepal color is invariant, or nearly so, in some populations (populations 1–7, 10). The metric characters, lateral sepal length and lower

Table 1. Floral Characters used to Distinguish the Three Subspecies of *Delphinium variegatum* (Summarized from Warnock 1990b, 1993, 1997).

| Floral character | *Delphinium variegatum* | | |
	ssp. *kinkiense*	ssp. *thornei*	ssp. *variegatum*
Sepal color	white to light blue (or lavender)	light blue to bright blue	deep royal blue, rarely white or lavender
Lateral sepal length	11–18 mm	17–21 mm	10–25 mm
Lower petal blade length	4–9 mm	6–11 mm	4–11 mm

TABLE 2. POPULATION NUMBER, SUBSPECIES DESIGNATION, COLLECTION LOCATIONS, APPROXIMATE POPULATION SIZES (1996), AND SAMPLE SIZES OF DELPHINIUM VARIEGATUM. San Clemente Island populations are listed north to south.

Population number	Subspecies	Location	Population size	Sample size
Island				
1	*kinkiense*	Flasher Canyon	200	28
2	*kinkiense*	Nots Drive	200	41
3	*kinkiense*	Pelican Canyon	2500	44
4	*kinkiense*	Larkspur Canyon	150	40
5	*kinkiense*	Stone Canyon	500	37
6	*kinkiense*	Burns-Horton Canyon	>1000	40
7	*kinkiense*	Lower Twin Dams Canyon	16	9
8	mix	Boulder	200	40
9	mix	Upper Twin Dams Canyon	1000	39
10	*kinkiense*	Warren Canyon	200	37
11	*thornei*	Upper Middle Ranch Canyon	75	32
12	mix	Lower Middle Ranch Canyon	350	32
13	*kinkiense*	Waynuk Canyon	1000	41
14	*thornei*	North Norton Canyon	60	17
15	*thornei*	South Norton Canyon	500	36
16	*thornei*	Horse Canyon	16	6
17	*thornei*	Box Canyon	150	30
18	*thornei*	Cave Canyon	400	37
19	*thornei*	Eagle Canyon	150	38
20	*thornei*	Eagle-Bryce Canyon	7	6
21	*thornei*	Bryce Canyon	200	39
22	*thornei*	Malo	300	31
23	*thornei*	Canchalagua Canyon	3000	40
24	*kinkiense*	Guds	75	35
Mainland				
1	*variegatum*	Edgewood County Park	200	33
2	*variegatum*	China camp State Park	100	38
3	*variegatum*	Green Springs Road	40	22
4	*variegatum*	Chinese Station	200	40
5	*variegatum*	Route 49	150	39
6	*variegatum*	Nacimiento-Ferguson Road	200	31
7	*variegatum*	G14	250	39

petal blade length, are highly variable in most populations, with largely overlapping ranges.

Mainland populations show a similar pattern (Fig. 3). Sepal color is relatively invariant in mainland populations with the exception of China Camp State Park, in which many white-flowered individuals occurred (18 of the 38 sampled). Mainland populations also show variation in metric characters, but they generally have narrower distributions with fewer outside values. Edgewood County Park has longer lateral sepals and lower petal blades than the other mainland populations.

Histograms of the three floral characters indicate lighter-colored and larger flowers for the island populations (treated together because of the broadly overlapping distributions noted above) than for mainland populations (Fig. 4). Sepal color is distributed bimodally on the mainland only because of white-flowered individuals in China Camp State Park. The distribution of sepal color on San Clemente Island is clearly bimodal, with 375 of the 775 individuals sampled (48.4%) having white or very light blue flowers (henceforward "light-flowered"; brightness values from 88–100), 72 (9.3%)

being intermediate (brightness values 56–87), and 328 (42.3%) having bright blue flowers (henceforward "dark-flowered"; brightness values 28–55). In contrast, the metric characters have unimodal distributions.

The overall bimodal distribution of sepal color on San Clemente Island shows a geographic pattern. Northern populations generally contain primarily light-flowered individuals and southern populations generally contain primarily dark-flowered individuals (Fig. 5). Central populations may contain substantial numbers of both flower types as well as intermediates.

Association among floral characters. The lateral sepal lengths of San Clemente Island individuals with light (brightness values 88–100) and dark (brightness values 28–55) sepal colors are significantly different (t = −5.78, df = 698, P < 0.0001), but their means (16.31 mm and 17.07 mm, respectively) and ranges (12.0–21.75 mm and 10.75–24.25 mm, respectively) are very similar. Likewise, lower petal blade lengths are significantly different for the two brightness classes (t = −6.11, df = 689,
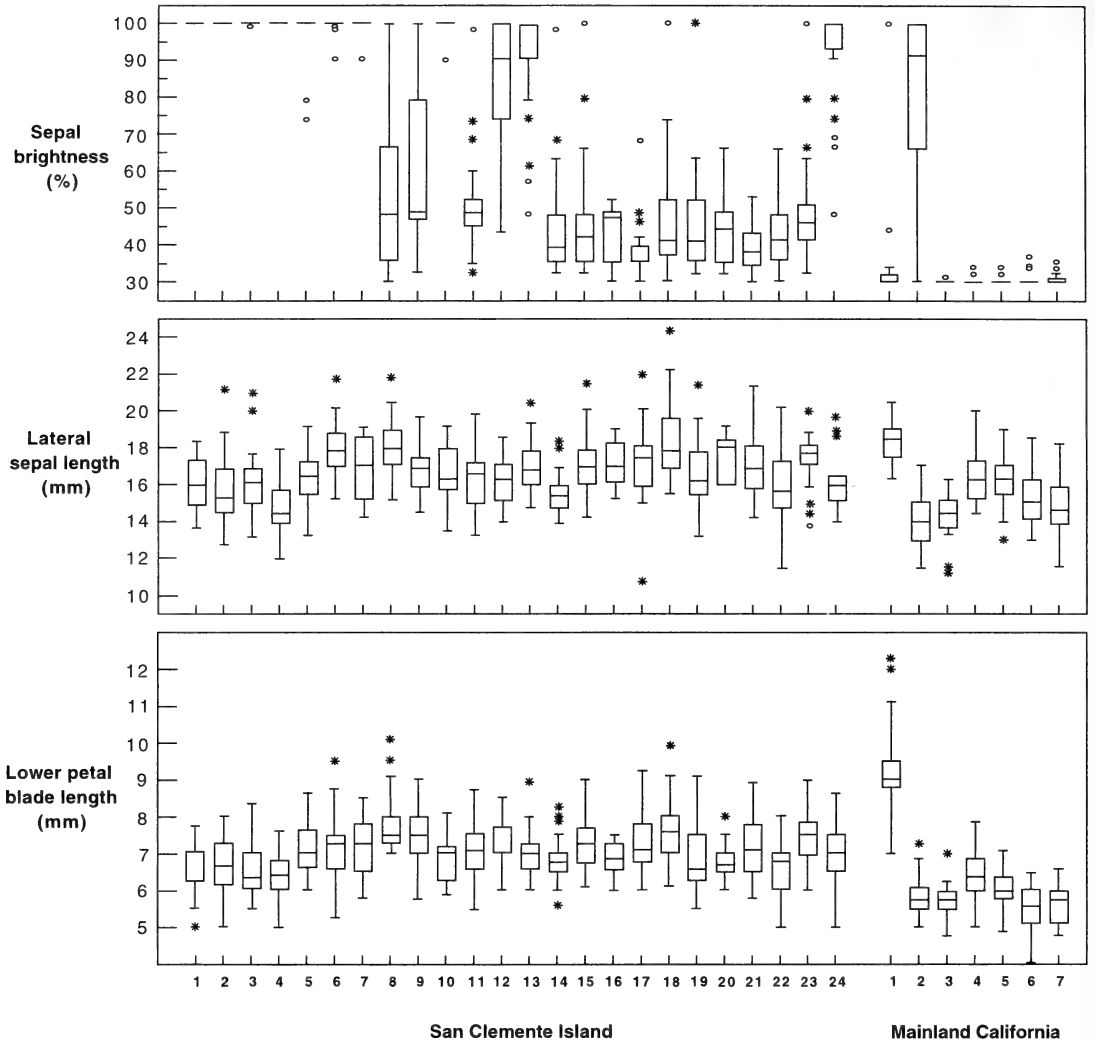
Fig. 3. Box plots of (a) brightness, (b) lateral sepal length, and (c) lower petal blade length in populations of *D. variegatum*. Median values (central line, defining the 50th percentile), upper and lower hinges (edges of the central box, defining the 25th and 75th percentiles), whiskers (extending to the farthest observation from the hinges not farther than 1.5 times the distance between the hinges), outside values (asterisks, observations farther from the hinges than 1.5 times the distance between the hinges), and far outside values (open circles, observation farther from the hinges than 3.0 times the distance between the hinges) are illustrated.

P < 0.0001), but their means (6.86 mm and 7.22 mm, respectively) and ranges (5.0–9.5 mm and 5.0–10.12 mm, respectively) are almost identical. Three of the four means fall within the overlapping portion of the ranges described for the two subspecies (Warnock 1990b, 1993, 1997).

A strong correlation exists between lateral sepal length and lower petal blade length (Pearson's r = 0.619, P < 0.0001; Fig. 6). Weaker correlations exist between brightness and lateral sepal length (Pearson's r = −0.213, P < 0.0001) and between brightness and lower petal blade length (Pearson's r = −0.216, P < 0.0001).

PCA groups individuals primarily by flower color with a broad range of lateral sepal and lower

petal blade lengths for each color class (Fig. 7). The first two axes account for 58.11% and 29.20% of the total variation, for a total of 87.31%. Plots of the first and third and of the second and third axes (not illustrated) are dense clouds of points showing no structure.

The deep royal blue sepal color of *D. v. variegatum* is significantly different from both light-flowered and dark-flowered island plants (mean = 38.19, range = 30.0–100.0; F = 1778.9, df = 2, r^2 = 0.798, P < 0.0001; Tukey HSD multiple comparison P < 0.0001 for both comparisons). Lateral sepals in *D. v. variegatum* are significantly shorter than in light-flowered and dark-flowered island plants (mean = 15.66, range = 11.25–20.5; F =
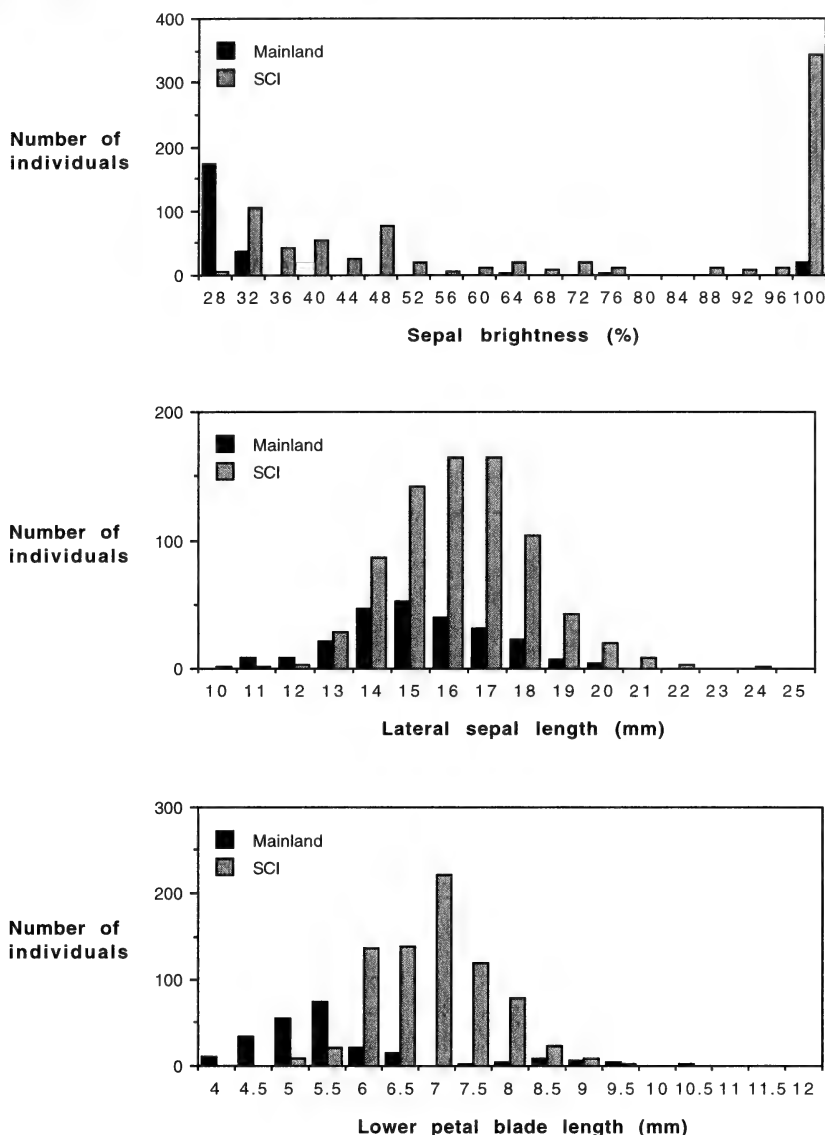
Fig. 4.   Histograms of brightness, lateral sepal length, and lower petal blade length for populations of *D. variegatum* on San Clemente Island. X-axis values represent the minimum of a class.

37.2, df = 2, r^2 = 0.076, P < 0.0001; Tukey HSD multiple comparison P < 0.0001 for both comparisons). Lower petal blades are also significantly shorter in *D. v. variegatum* (mean = 6.34, range = 4.00–12.15; F = 47.7, df = 2, r^2 = 0.097, P < 0.0001; Tukey HSD multiple comparison P < 0.0001 for both comparisons).

DISCUSSION

Floral variation. All three floral characters exhibit substantial variation within populations. The metric characters, lateral sepal length and lower petal blade length, exhibit unimodal distributions both on the mainland and on San Clemente Island. Mainland populations have smaller flowers than is-

land populations, with the exception of Edgewood County Park in which lower petal blades lengths even exceed those of San Clemente Island plants.

Sepal color is relatively invariant on the mainland, although it shows a bimodal distribution due to the high proportion of white-flowered individuals in China Camp State Park. In contrast, sepal color is clearly bimodally distributed on San Clemente Island. Most island populations of *D. variegatum* are highly variable in sepal color, although some consist primarily of white-flowered individuals.

Floral characters and taxonomy. Warnock (1990b) divided *D. variegatum* into three subspecies primarily on the basis of sepal color, lateral sepal length, and lower petal blade length. The
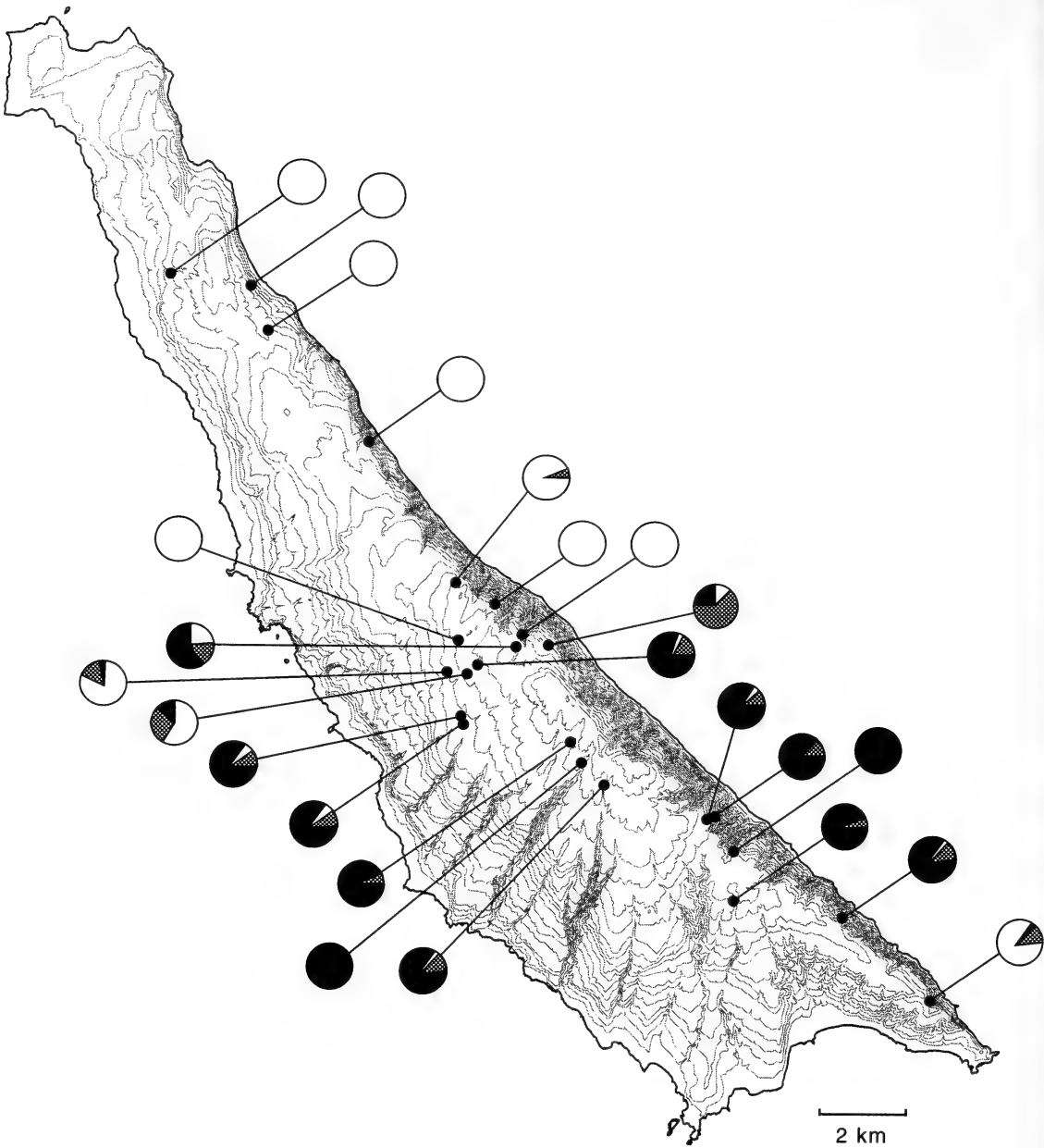
Fig. 5. Pie charts of flower color in San Clemente Island populations of *D. variegatum*. White areas represent proportion of individuals with white or light blue flowers (brightness values from 88 to 100), black areas represent individuals with bright blue flowers (brightness ≤55), and stippled areas represent individuals with intermediate colors (brightness values from 56 to 87).

mainland populations we sampled generally fit Warnock's (1990b) descriptions of *D. v. variegatum* (Table 1), although some individuals in Edgewood County Park have lower petal blade lengths exceeding the described taxonomic range. *Delphinium v. variegatum* differs from the two island subspecies in generally having darker (deep versus bright blue) flowers (except for many individuals in China

Camp State Park) and shorter lower petal blades (except in Edgewood County Park).

Considerable population differentiation appears to exist within *D. v. variegatum*. Of the seven populations we sampled, two are morphologically distinct: China Camp State Park has a high proportion of white-flowered individuals (absent in the other populations we sampled), and Edgewood County
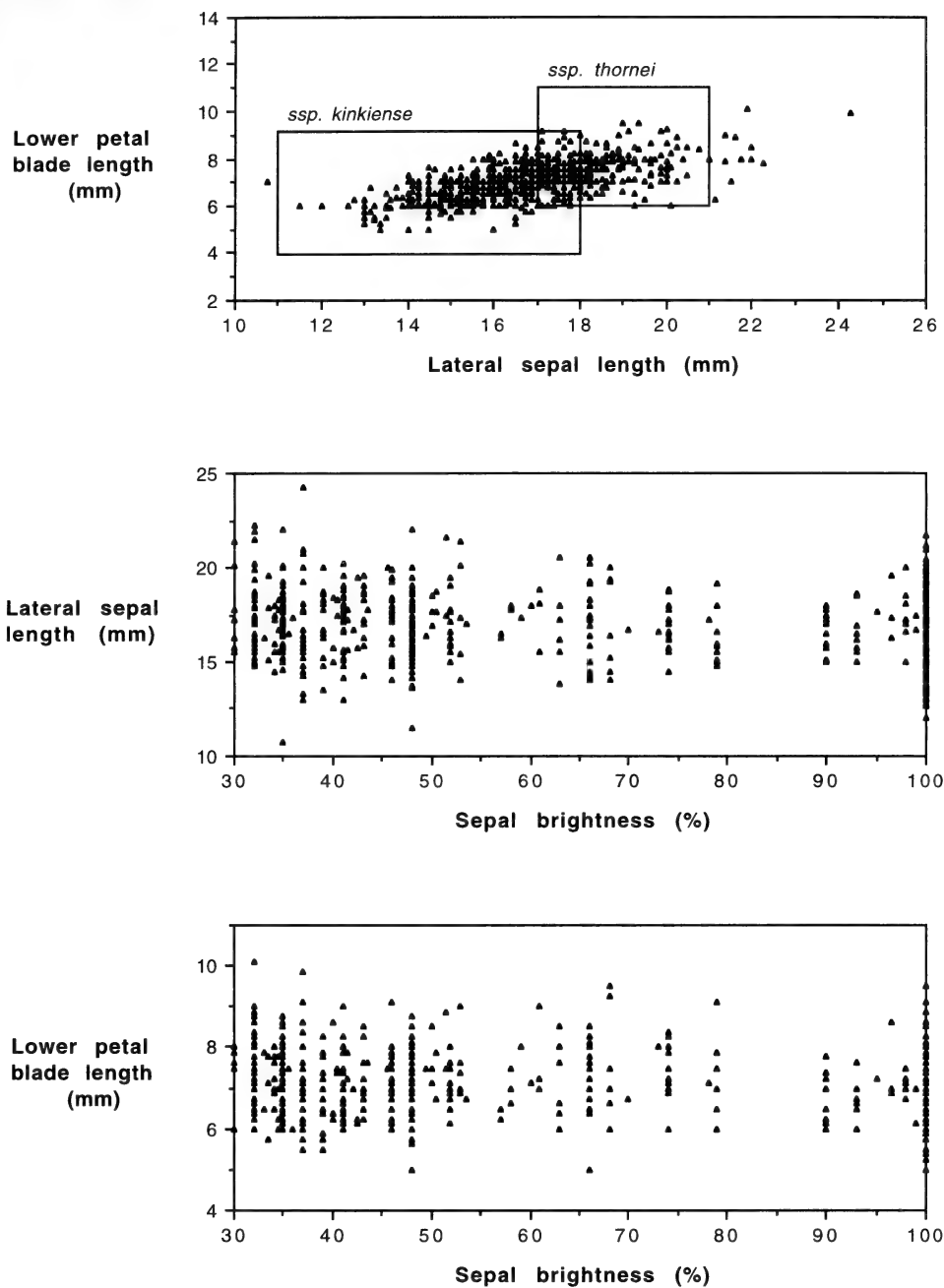
Fig. 6.   Scatterplots of sepal brightness, lateral sepal length, and lower petal blade length for individuals of all populations of *D. variegatum* on San Clemente Island. Taxonomic designations shown are from Warnock (1990b, 1993, 1997).

Park has larger flowers than other populations. Subsequent to sampling, we discovered that Edgewood Park is the only population we sampled that occurs on serpentine soils. Warnock (1990b) considers serpentine soil populations of *D. v. variegatum* to be not well marked morphologically and did not recognize them as distinct taxa. Instead, Warnock (1997) comments that plants with large flowers are

common in the San Francisco Bay area, either as scattered individuals or as populations made up largely of such individuals. In other species, plants growing on serpentine soils have often been documented to be morphologically and genetically distinct from plants growing on non-serpentine soils (Kruckeberg 1954; Mayer et al. 1994). Intensive sampling of additional natural populations of *D. v.*
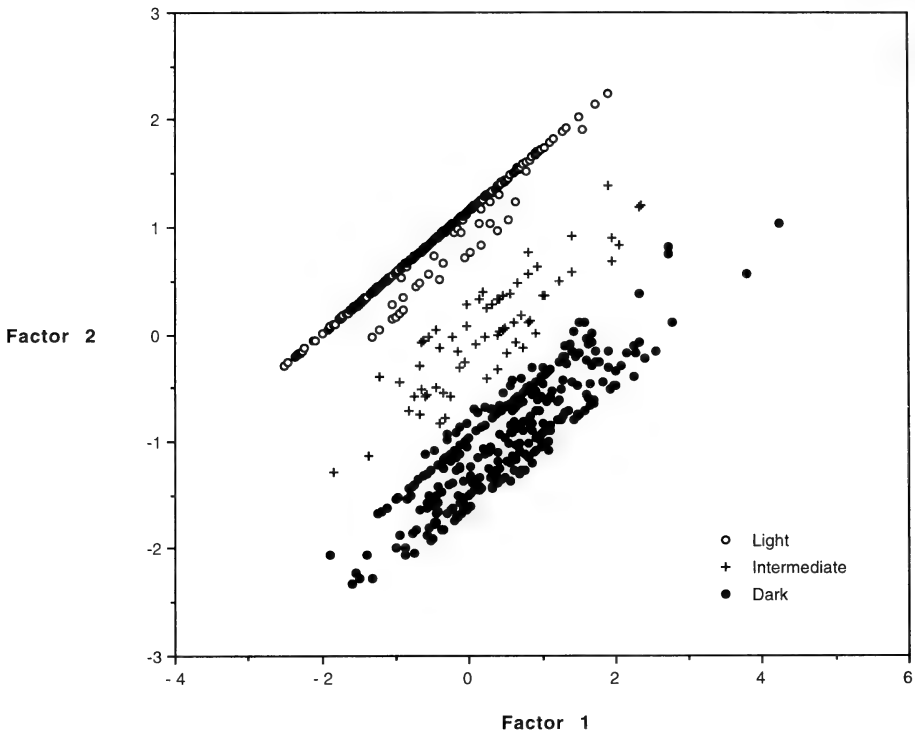
Fɪɢ. 7. Scatterplot of the first and second PCA axes for floral characters in *D. variegatum* on San Clemente Island. Individuals are coded as having light (brightness values 88–100), intermediate (brightness values 56–87) or dark (brightness values 28–55) flower color.

variegatum may clarify whether serpentine soil populations are differentiated morphologically from non-serpentine soil populations or whether variation is geographic in pattern.

Delphinium v. kinkiense and *D. v. thornei* also generally conform to Warnock's (1990b, 1993, 1997) descriptions, in spite of some individuals having lateral sepals exceeding the described taxonomic range (Fig. 6). However, our data do not support the separation of *D. v. kinkiense* and *D. v. thornei* on the basis of all three floral characters. Specifically, our results indicate that the two metric characters, lateral sepal length and lower petal blade length, provide no clear distinction between these taxa. Both exhibit a unimodal distribution on San Clemente Island so that any attempt to use them for delineating taxa is necessarily arbitrary. In addition, the majority of individuals fall within or near the area of overlap for these characters.

Both lateral sepal length and lower petal blade length show a statistically significant association with sepal color, indicating that light-colored flowers tend to be smaller than dark-colored flowers. These results are in agreement with Warnock's (1990b) descriptions. However, their significance should be considered an artifact of large sample size. The almost identical means and almost completely overlapping ranges of the metric characters for light- versus dark-colored flowers indicate that

the statistical differences have little taxonomic significance.

The remaining floral character, sepal color, is the least ambiguous for differentiating between *D. v. kinkiense* and *D. v. thornei* but it is also problematic, exhibiting a more complex pattern of variation on San Clemente Island than previously suspected. Although northern populations generally contain primarily light-flowered individuals and southern populations generally contain primarily dark-flowered individuals, central populations may contain substantial numbers of both flower types as well as intermediates. Moreover, this is only a general trend as the southernmost population (Guds) is predominantly, although not exclusively, light-flowered. In addition, nearly half of the populations (11 of 24) contain both light- and dark-flowered individuals, thus having individuals with sepal colors considered to represent different subspecies. The complex pattern of variation observed for sepal color on San Clemente Island may be due to hybridization and subsequent introgression between the taxa. Genetic data may provide evidence regarding this possibility.

The discrepancy between our results and the taxonomic separation of *D. v. kinkiense* and *D. v. thornei* is probably due to our intensive sampling of all natural populations of *D. variegatum* on San Clemente Island. The taxonomic descriptions of these

taxa are based on examination of herbarium specimens (M. Warnock, University of Missouri, Columbia, pers. comm.) that may have represented only a fraction of the variation found in natural populations. This is clearly a potential problem with any taxon endemic to remote locations, especially in cases where access is highly restricted (permission of the U.S. Navy is required to visit San Clemente Island).

Classification of San Clemente Island populations. Because *D. v. kinkiense* is listed as endangered and *D. v. thornei* is merely considered a species of concern by the USFWS, it is necessary for practical reasons to identify populations on San Clemente Island. Since our analyses show poor separation between subspecies for lateral sepal and lower petal blade lengths, sepal color was used to classify populations as *D. v. kinkiense, D. v. thornei,* or mixed. Populations having at least 80% light-flowered individuals (brightness values between 88 and 100) were classified as *D. v. kinkiense,* and populations having at least 80% dark-flowered individuals (brightness values below 56) were classified as *D. v. thornei*. Populations with less than 80% of its individuals in either brightness range were classified as mixed. This criterion is based on the observed bimodal distribution of sepal color. Using this criterion, there are 10 populations of *D. v. kinkiense,* 11 populations of *D. v. thornei,* and 3 mixed populations (Table 2, Fig. 5).

Although an 80% criterion seems to be a weak basis for distinguishing taxa, it may be preferable to a stricter classification. If Warnock's (1990b, 1993, 1997) descriptions are interpreted in conjunction with the bimodal distribution we have documented, then individuals with brightness values from 88 to 100 may be classified as *D. v. kinkiense* (white to light blue flowers) and individuals with brightness values below 88 may be classified as *D. v. thornei* (light blue to bright blue flowers). Using this criterion, there are 7 populations of *D. v. kinkiense,* 5 populations of *D. v. thornei,* and 11 mixed populations (Fig. 5).

The results of this study indicate that *D. v. kinkiense* and *D. v. thornei* are, at best, currently separable only on the basis of sepal color. They may be more appropriately classified as varieties rather than subspecies or classified together as one subspecies (as defined by Stuessy 1990). However, it is not uncommon for plant taxa to be separated on the basis of morphological characters controlled by only one or two loci, such as flower color (Bachmann 1983; Gottlieb 1984; Hilu 1983). Moreover, other characters such as flowering time may clearly distinguish *D. v. kinkiense* and *D. v. thornei*. The northern populations of predominantly light-flowered individuals flower earlier than the southern, dark-flowered populations (S. Junak, Santa Barbara Botanic Garden, pers. obs.), although this may have an environmental rather than a genetic basis. Further taxonomic study using additional characters should be conducted to decide whether the island taxa have been appropriately designated as separate subspecies. Correct taxonomic designation has practical implications for the survival of these taxa because only *D. v. kinkiense* has legal protection.

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CROWN STRUCTURE OF THE WORLD'S SECOND LARGEST TREE

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Abstract

We studied the crown structure of the Washington Tree (*Sequoiadendron giganteum* (Lindley) Buchholz) in Sequoia National Park, California. The tree was 77.3 m tall and 9.1 m basal diameter. Its total volume was 1403.2 m^3, including the main trunk (1357.3 m^3) and 46 reiterated trunks (45.8 m^3). The main trunk was hollow, and 133.2 m^3 of wood volume was missing. A 35-m deep, 2–3-m wide pit extended into the heart of the main trunk below 58 m. The microclimate at the bottom of the pit was dark, cool, and humid. Fire and fungal decay apparently contributed to the formation of the pit. Some charred wood was evident throughout the pit, but most of this had fallen away and been replaced by decayed wood. The walls of the pit in the lower 17 m were spongy, wet, and covered by fungal mycelia.

Sequoiadendron giganteum (Lindley) Buchholz (giant sequoia) is an awe-inspiring species restricted to 66 groves in California's Sierra Nevada (Willard 1995). These are the world's largest living trees (Flint 1987), and some individuals are over 3000 years old (Hartesveldt et al. 1975). As such, they have attracted a great deal of scientific interest. They were among the earliest trees in North America to be studied from a canopy perspective; rope techniques and an elevator were used to sample cones and arboreal arthropods in the 1970's (Harvey et al. 1980). However, the crown structure of ancient *S. giganteum* trees has never been studied.

The crown structure of ancient *Sequoia sempervirens* (D. Don) Endl. trees, the closest living relatives of *S. giganteum,* has recently been the focus of research (Sillett 1999). Like many other conifers, including *S. giganteum, S. sempervirens* grows via a simple architectural model consisting of a vertical trunk that supports numerous horizontal branches. Ancient trees, which have endured centuries of wind and fire, develop highly individualized crowns consisting of multiple, resprouted trunks (i.e., vertically oriented stems) arising from other trunks and branches. One very complex *S. sempervirens* tree, for example, has a crown with 148 resprouted trunks accounting for over 14 percent of its total wood volume (Sillett and Van Pelt 2000). Such extra trunks are reiterations of the tree's architectural model (Hallé et al. 1978). They are indistinguishable from free-standing trees except for their locations within the crown of a larger tree. Each reiterated trunk supports its own system of horizontal branches.

This is the first rope-based study of crown structure in an ancient *S. giganteum* tree. We used methods developed in *S. sempervirens* to map the crown of the Washington Tree, the second largest *S. giganteum* tree (Flint 1987). Our objective was to calculate the tree's total volume, including reiterations. During our exploration of the tree, we discovered a deep pit extending into the heart of the tree's main trunk. We compared microclimatic conditions inside the pit with those on top of the crown.

Study Area

The Washington Tree is located at 2085 m elevation near the center of Giant Forest in the southern Sierra Nevada of California (36°33′N, 118°45′W). At 1212 hectares, Giant Forest is the second largest of the unlogged *S. giganteum* groves (Willard 1995). The average temperature ranges from 0.2°C in January to 17.9°C in July with an annual average of 8.1°C. Much of the area's 110 cm precipitation falls as snow (482 cm average accumulation), and a snowpack persists into spring. The summer is very dry; only 2 cm of precipitation falls between July and September (National Park Service).

The Washington Tree grows near a large granite outcrop in a forest dominated by *S. giganteum, Abies concolor* (Gordon & Glend.) Lindley, and *Pinus lambertiana* Douglas. The area has been burned within the last 15 years as part of a prescribed burning program carried out by the National Park Service. Abundant regeneration of *S. giganteum* and *P. lambertiana* is visible in the vicinity of the Washington Tree and the nearby Franklin Tree.

Methods

Tree access. We accessed the Washington Tree by shooting a rubber-tipped fiberglass arrow trailing 10 kg test strength Fireline® filament over sturdy branches with a compound bow mounted to a spinning reel. A 3 mm nylon cord, followed by a 10 mm static kernmantle climbing rope, was then hauled over the branches. We anchored one end of
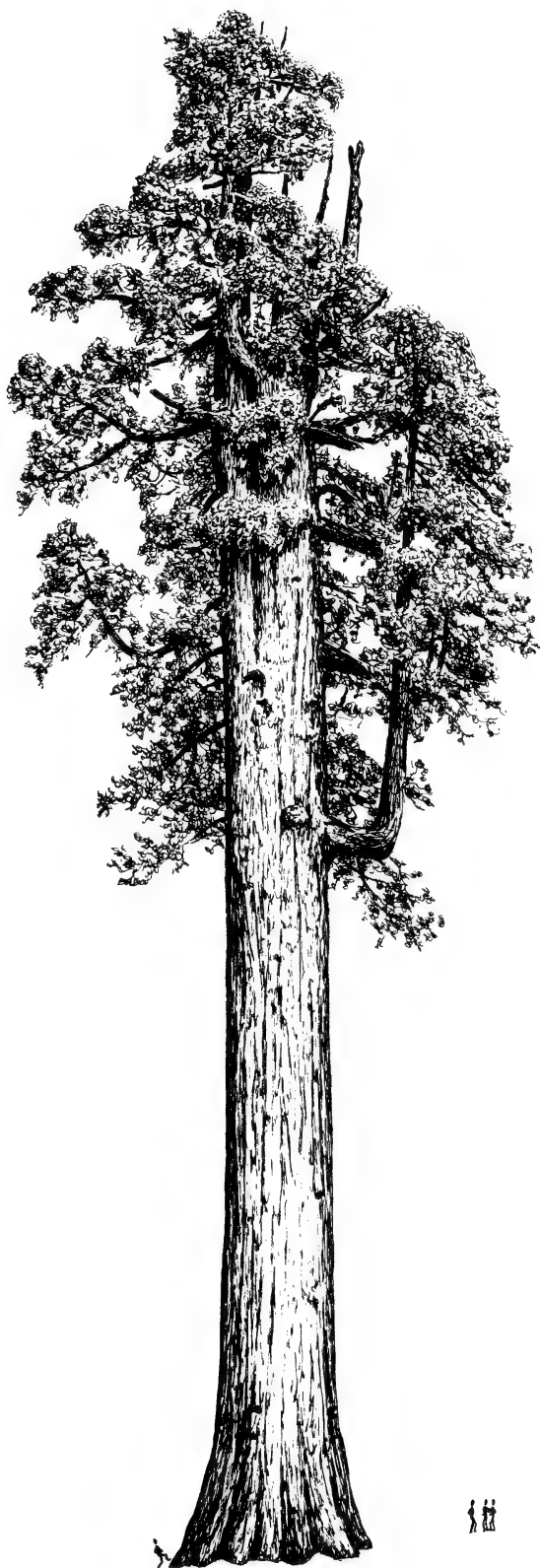
the rope at ground level and climbed the other using mechanical ascenders. We used a 20 m long arborist's rope lanyard to access progressively higher branches and to move laterally through the crown. We worked in the tree crown during a two-week period from May to June 1999.

Crown mapping. We mapped crown structure of the Washington Tree by measuring dimensions of the main trunk and all reiterated trunks (both living and dead) over 5 cm basal diameter. All trunk diameters were measured directly using a graduated tape. The main trunk's diameter was measured at the highest ground surface, which was 0.65 m above true ground level (i.e., the average of the highest and lowest ground surfaces), at 2.5 m intervals from true ground level to 15 m, and at 5 m intervals above 15 m. Branches and reiterated trunks prevented us from obtaining diameter measurements at every height interval. In these cases, we measured trunk diameter as close to the regular interval as possible. Since the main trunk was hollow (see RESULTS), we also measured the maximum and minimum diameters of the hollow cavity at 5 m intervals.

A series of reiterated trunks extended well above the broken top of the main trunk. The tree's total height was measured by lowering a tape from the topmost foliage to true ground level. We recorded the following data for each reiterated trunk: top height, height of origin, basal diameter, and diameter at 5 m intervals along the length of the trunk. For reiterated trunks arising from branches, we also recorded horizontal distance to main trunk, branch height, branch basal diameter, and branch diameter at reiteration. We only surveyed branches giving rise to reiterated trunks; no other branches were measured. Reiterated trunks were referenced to the main trunk by recording azimuths and distances between them at 5 m height intervals. We used an Impulse® laser range finder (Laser Technology, Inc.) to measure horizontal distances between trunks. All other measurements were made with the aid of a compass, clinometer, and graduated tape. Since large trunks often gave rise to smaller trunks, we sketched crown structure and noted physical connections between trunks and branches. We also noted whether trunks were monopodial (i.e., consisting of a single axis), sympodial (i.e., consisting of successive axes), or otherwise broken. All information was used to generate a tree crown diagram.

Crown illustrations. We made an illustration of the entire Washington Tree from the ground. Major branches, clumps of foliage, burls, and kinks were

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Fig. 1. Illustration of the Washington Tree prepared by Robert Van Pelt on the basis of crown structure data and photographs taken from the ground.

noted on a sketch, and heights to these landmarks were measured with the Impulse® laser. We then took photographs of all portions of one side of the crown from as far away from the tree as possible. The illustration itself started with a "skeleton," which was based on the height and diameter measurements taken both from within the crown and from the ground. We used the photographs to provide details of foliage, branches, and bark texture. The illustration was drawn at $\frac{1}{120}$ scale, and human figures were added for additional scale. We also made a detailed illustration of the upper crown, including the entrance to the pit. Photographs and sketches made from a nearby hill supplemented sketches made from within the tree crown.

Microclimate sampling. We measured light, air temperature, and relative humidity at three positions in the tree's crown. Sensors were lashed to the tree's uppermost branches with nylon cord to obtain measurements from the top of the crown (77 m). Sensors were suspended on a rope to obtain measurements from the top of the pit (57 m) and the bottom of the pit (23 m). Microclimate measurements were made at 4-minute intervals over a 23-hour period (11 a.m. June 11 to 10 a.m. June 12). We used HOBO® RH/Temp Loggers to measure air temperature and relative humidity and StowAway® Light Intensity Loggers to measure light intensity (Onset Computer Corporation).

Calculations. We used Wendell Flint's ground-level survey data for Washington Tree (Flint unpublished) to determine the basal diameter of the main trunk. Direct tape measurements overestimate basal area by failing to account for missing wood in fire cavities and spaces between buttresses. We calculated the surface area of the tree's "footprint" and converted this to a true basal diameter (diameter = 2[footprint area/π]$^{1/2}$). Trunk volume was calculated by applying two different equations to the trunk diameter data. We used the equation for a parabolic frustum (i.e., volume = length/2*[A1 + A2], where A1 and A2 are the upper and lower trunk cross sectional areas) for sections of trunks that tapered slowly. We used the equation for a regular conic frustum (i.e., volume = length*π/3*[lower diameter^2 + (lower diameter)*(upper diameter) + upper diameter^2]) for sections of trunks that tapered more rapidly, such as within the crown. Using the latter equation, we also calculated the volume of branches supporting reiterations based on the limited data we collected on these branches (see above).

RESULTS

Volume. The Washington Tree is 77.3 m tall and 9.1 m basal diameter (Fig. 1). A large fire cave has been burned away from the main trunk near the ground. It consists of an inner portion that is 3.7 m high, 2.4 m wide, and 2.6 m deep as well as an outer portion that is 5.8 m high, 4.2 m wide, and 0.5 m deep. Above 58 m, the main trunk is broken (Fig. 2). A shield of wood extends 10 m above this break and terminates two structures: a partially dead reiteration and the splintered remains of the main trunk. According to our calculations, the Washington Tree's main trunk has a volume of 1357.3 m^3, including the volume occupied by the pit (see below). Reiterated trunks (see below) add an additional 45.8 m^3 of volume, the three largest reiterations accounting for 79.6 percent of this total. Thus, the Washington Tree's total trunk volume is 1403.2 m^3. Branches bearing reiterations on the Washington Tree (n = 22) add an additional 25.6 m^3 volume, but we emphasize that our measurements of branch volume are incomplete.

Reiterations. The Washington Tree has 46 reiterated trunks arising from the main trunk (n = 3), other trunks (n = 10), and branches (n = 33) (Figure 2). The largest reiteration, which is 1.7 m basal diameter and 16 m long, sprouts from the main trunk at the mouth of the pit and terminates in a dead broken stump that is 0.8 m diameter. It supports 19 other trunks, including two dead and seven sympodial trunks. Like the main trunk, the largest reiterated trunk is hollow with a lesser pit that is 5.1 m deep. Another large reiteration sprouts from the end of a 1.1 m diameter branch emanating from the main trunk at the mouth of the pit. Its top is dead, and it supports four other trunks. Eight trunks emerge from the backside of the shield above the pit. Two of these trunks are completely dead, and two have dead tops. All of the rest of the Washington Tree's reiterations arise from branches emanating from the main trunk. The largest of these trunks is 1 m basal diameter and 25.2 m long. It sprouts from the end of a 4 m long, 1.2 m diameter branch at 35.7 m above the ground. The Washington Tree's largest branch, which supports three trunks, is 1.4 m basal diameter, 10 m long, and located 45.4 m above the ground.

The pit. A 35-m-deep pit extends down into the heart of the Washington Tree from the break in its main trunk below the shield (Figs. 2 and 3). The pit is over 2 m diameter at the mouth, and it enlarges to over 3 m diameter farther down. At the bottom (i.e., 22.8 m above ground level), the pit is 3.05 by 0.62 m wide. Charred wood is evident along the walls of the pit throughout most of its length, and fungal decay becomes pronounced with increasing depth. Below 40 m, fungal mycelia are evident along the walls, and the wood is soft and wet. Humus has accumulated on ledges of rotting wood. Massive protrusions of dead wood extend from the walls of the main trunk into the pit, evidence of ancient branch bases. At the bottom of the pit, these branch bases are small, and the humus is deep, rich, and filled with rotting seed cones. Annual rings are visible in the spongy wood, some of them perhaps 3000 years old (Stephenson in press). The pit occupies 133.2 m^3, or about 10 percent, of
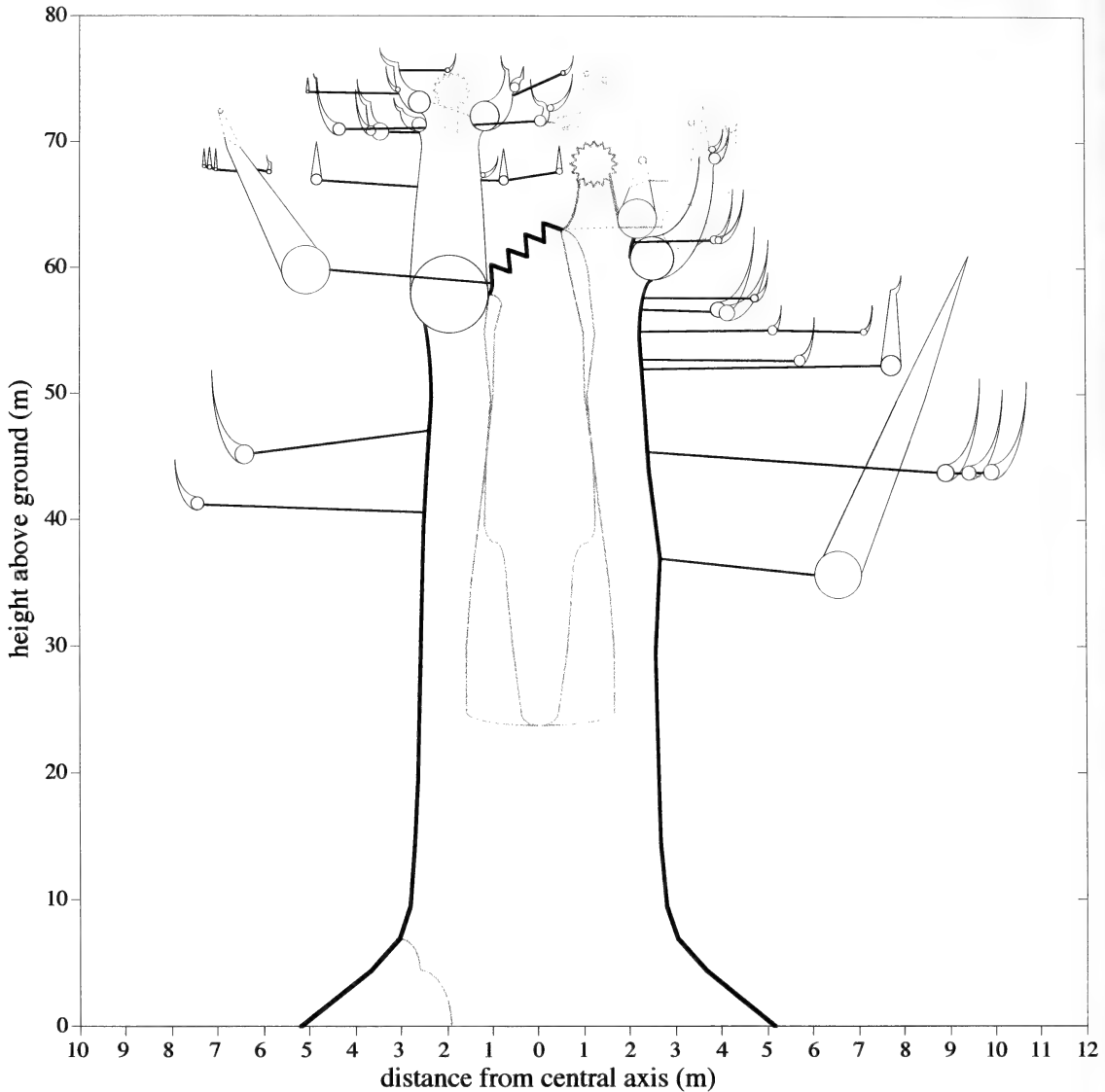
Fig. 2. Crown diagram of the Washington Tree. All trunk diameters are drawn to the scale of the x-axis, which is expanded relative to the scale of the y-axis. Circles correspond to the basal diameters of reiterated trunks. Serrated edges indicate broken trunks. Branches bearing reiterated trunks are depicted with single straight lines. No other branches are shown. Gray lines indicate dead branches and trunks. Gray lines also indicate a basal fire cavity as well as maximum and minimum diameters of the pit.

the main trunk's volume. Thus, the Washington Tree's total wood volume is 1270.0 m³.

There are two narrow fissures in the main trunk far above the bottom of the pit (i.e., 59.5–51.7 m and 36.3–33.4 m). The upper fissure is located in a large area of dead wood on the outside of the main trunk that extends from the shield to 49.4 m above the ground. Some light and wind pass into the pit through the opening, which is up to 10 cm wide. The lower fissure is much narrower. It affords no breeze, but there is enough light to support an epixylic green alga on the inner surface of the opening.

Microclimate. At the bottom of the pit, the microclimate was relatively dark, cool, and humid during the 23-hour sampling period. Light intensity during the day was less than 0.1 percent as high as on top of the crown and less than 1 percent as high as on top of the pit. Temperatures at the bottom of the pit remained a constant 4°C for the duration of the sampling period. The other locations were 4.5 to 11°C warmer than the bottom of the pit. The top of the pit was 0.5 to 3°C cooler during the day and up to 2°C warmer during the night than the top of the crown. Relative humidity at the bottom of the
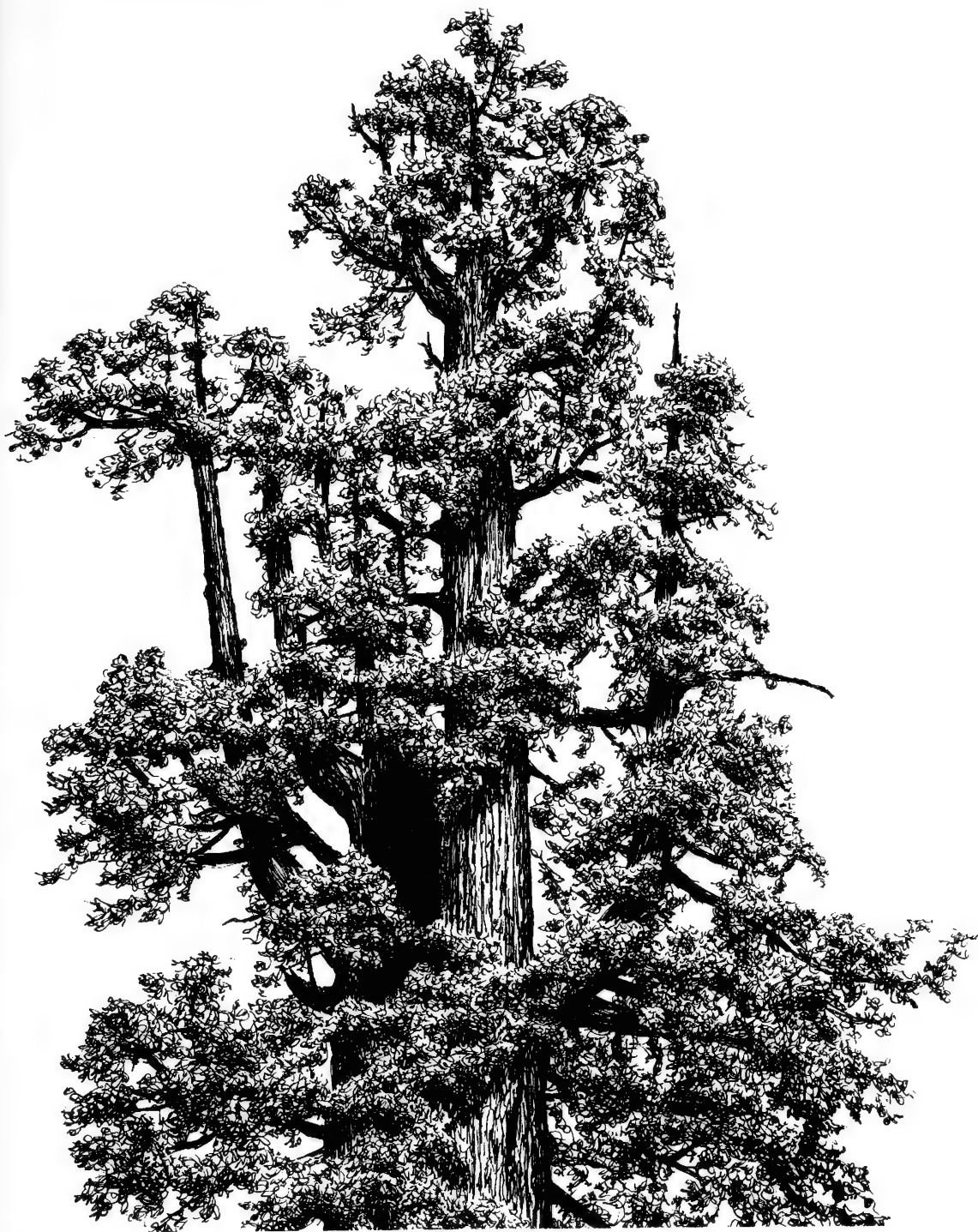
FIG. 3. Detailed illustration of the Washington Tree's upper crown, including the mouth of the pit, prepared by Robert Van Pelt on the basis of crown structure data and photographs. This view is from a location 120° clockwise of the view in Figure 1.

pit remained a constant 99 percent for the duration of the sampling period. The other locations were 23 to 60 percent less humid than the bottom of the pit. The top of the pit was 5 to 25 percent more humid during the day and up to 10 percent less humid during the night than the top of the crown.

DISCUSSION

Tree size. The Washington Tree has been known as the world's second largest tree for over a decade (Flint 1987), and our direct crown-level measurements confirm this fact. Among living trees, only the General Sherman Tree, whose main trunk has a volume of 1489 m³, is larger (Van Pelt in press). The main trunk of the General Grant Tree, whose volume is 1357.3 m³, is identical in volume to the Washington Tree's main trunk, but the General Grant Tree has a smaller volume of reiterated trunks (Van Pelt in press). However, the Washington Tree's total *wood* volume, including reiterations, is actually less than that of the General Grant Tree, the President Tree (1318.0 m³, Van Pelt in press), and the Lincoln Tree (1275.2 m³, Van Pelt in press) because its main trunk is hollow.

Among living *S. giganteum,* many trees are taller than the Washington Tree, and several trees (e.g., Ishi, Grant, and Boole) have larger bases (Van Pelt in press). The Washington Tree, however, is the largest living tree from 3.2 to 4.3 m (main trunk diameters 7.6 to 7.0 m) and from 50.0 to 58.5 m (main trunk diameters 4.6 to 3.8 m) above the ground. Prior to losing the upper part of its main trunk, the Washington Tree may have been the only living tree larger than the General Sherman Tree (Flint 1987).

Crown structure. Like their close relative, *Sequoia sempervirens,* ancient *Sequoiadendron giganteum* trees can have complex crowns consisting of multiple reiterated trunks. Ancient trees of both redwood species frequently possess branches that gradually curve upwards and become increasingly trunk-like over time. Perfectly vertical reiterated trunks, however, appear to be less common on *S. giganteum* than on *S. sempervirens.* And unlike *S. sempervirens,* old *S. giganteum* branches tend not to be heavily buttressed; they appear almost circular in transverse section. Furthermore, flagelliform branches and fusions between trunks and branches, which are common in ancient *S. sempervirens* crowns (Sillett 1999; Sillett and Van Pelt 2000), are rarely encountered on *S. giganteum.*

It is difficult to compare the Washington Tree's crown structure with that of other ancient *S. giganteum* trees because no others have been thoroughly mapped using rope-based methods of access. Ground-level surveys permit a few preliminary comparisons. Unlike the Washington Tree, several of the largest *S. giganteum* trees (e.g., Grant, Lincoln, Stagg, Boole, Genesis) have very few (if any) reiterated trunks (Van Pelt in press). The General

Sherman Tree's crown, however, is highly reiterated, and a few of these reiterations are larger than any on the Washington Tree (Van Pelt in press). The Franklin Tree (1222.7 m³ volume, Van Pelt in press), which grows within 500 m of the Washington Tree, also has a highly reiterated crown, but nearly all of its large reiterations are dead.

Fire and fungi. Tops of the main trunks on many ancient *S. giganteum* trees are dead (Rundel 1973), and most trees have fire scars throughout their crowns. The Washington Tree is no exception. Trunks that have been hollowed out by fire are also commonly observed, but the Washington Tree's pit may be unique. In reference to hollow trunks, John Muir wrote, "All of these famous hollows are burned out of solid wood, for no Sequoia is ever hollowed by decay" (1909). He clearly never observed the Washington Tree's pit!

There is no doubt that fungal decay has played a major role in creating the pit; the heartwood is rotting and spongy, and fungal mycelia are abundant. Indeed, microclimatic conditions in the lower portion of the pit promote fungal decay. After the top of the main trunk broke away, fire probably initiated formation of the pit, perhaps via a mechanism similar to the one Muir observed on fallen logs during a fire (1909):

> *After the great glowing ends fronting each other have burned so far apart that their rims cease to burn, the fire continues to work on in the centres, and the ends become deeply concave. Then heat being radiated from side to side, the burning goes on in each section of the trunk independent of the other, until the diameter of the bore is so great that the heat radiated across from side to side is not sufficient to keep them burning. It appears, therefore, that only very large trees can receive the fire-auger and have any shell rim left.*

But precipitation accumulated in the newly formed pit, and the moist wood was ultimately colonized by decay fungi that increased its size over many years. Subsequent fires probably consumed much of the decaying wood (Piirto et al. 1984). We observed some charred wood on the walls of the pit to within 0.7 m of the bottom, so fire has clearly contributed to the hollowing of the pit to a great depth. However, most of the charred wood has fallen away and been replaced by decaying wood. Thus, both fire and fungal decay were directly involved in the formation of the pit.

viewers provided constructive comments on the manuscript. Finally, Wendell Flint graciously provided us with his ground-level survey data for the Washington Tree.

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ERIOGONUM SPECTABILE (POLYGONACEAE): A NEW SPECIES FROM NORTHEASTERN CALIFORNIA

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ABSTRACT

Eriogonum spectabile, a new species of the subgenus *Eucycla,* is described from northeastern Plumas County in northeastern California, USA. It differs from the related *E. pendulum* of northwestern California and adjacent southwestern Oregon in being a shorter, more compact plant with more numerous branches at the base, narrower leaves with the pubescence equally distributed on both surfaces, longer petioles, reduced umbellate inflorescences, broadly campanulate involucres, and densely pubescent flowers with gland-tipped hairs among the silky-white ones. The new species is currently known only in an extremely limited area of glaciated andesite southeast of Lassen Peak.

A new species of *Eriogonum* Michx. was encountered during project field surveys on the Lassen National Forest in northeastern California on 30 July 1997. This plant was immediately recognizable as distinctly different from other known *Eriogonum* species in this part of the state, and indeed from all other known *Eriogonum* by the combination of its low shrubby habit and densely pubescent flowers and fruits. Subsequent surveys have resulted in a total of only three occurrences with about 250 plants total, all within about 1 km of each other.

Eriogonum spectabile B. L. Corbin, Reveal, & R. Barron, sp. nov. (Fig. 1).—TYPE: USA, California, Plumas Co., ca. 13 km north of Chester, ca. 1.9 km west-southwest of Hay Meadows trailhead to the Caribou Wilderness, Lassen National Forest, T30N, R7E, sect. 28 NE ¼ of SW ¼, MDM, ca. 40°25′N, 121°12′W, 18 Aug 1998, *Corbin and Earll 910* (Holotype: US; Isotypes DAV, JEPS, K, MARY, NY, RSA, Lassen National Forest herbarium.)

Planta perennis, suffrutex, usque 2.5 cm alta; caules patentes dense ramosi fragiles; petioli breves 0.6–0.9 cm longi; lamina foliaris anguste elliptica, 0.5–1.7 cm longa, 0.4–0.7 cm lata, in superficiebus ambabus sericea cinereo-tomentosa, marginibus integris planis vel revolutis praedita. Caules florentes scaposi, primo albi-tomentosi deinde glabrati; inflorescentia umbellata; bracteae semifoliaceae, angusti-oblongae vel-ellipticae, albi-tomentosae; involucra solitaria, extus sericeo-tometosa atque dense gladularia intus glabra; dentes involucrales 5–7, acute triangulares, 1.0–1.2 mm longi; bracteolae numerosae lineares. Flores sub anthesi albi, sub gemmascentia frutescentiaque rosei vel subrubri, nervo medio fuscato ornati; tepala extus dense hirsuta intus subglabra, per anthesin 4.0–4.5 mm longa; stamina inclusa vel exserta; antherae rubrae vel purpureae. Achenia 3–4 mm longa, tomentosa, ad basem subglobosam in rostrum crassum 3-angulum contracta.

Plants low shrubs 1–1.5 dm high vegetatively and 1.7–2.5 dm high in flower, mostly 3–5.5 dm across; stems spreading, densely branched, brittle, arising from a stout, woody taproot (up to 5 cm across at the top of the taproot), the older branches with reddish-brown bark exfoliating in wide strips. Leaves arranged in open rosettes mostly at the base of the flowering stem or at the tips of exposed caudex branches, others sheathing shortly up the herbaceous stems; leaf blades narrowly elliptic, (0.7–)1.2–1.7(–2.2) cm long, (0.2–)0.4–0.7(–0.9) cm wide, equally densely gray and somewhat silky tomentose on both surfaces; leaf margins entire and plane to revolute; leaf apex broadly acute, the base cuneate. Petiole short, (0.2–)0.6–0.9(–1.3) cm long, silky tomentose. Petiole base elongate triangular, 3–5 mm long, 2–4 mm wide, densely white tomentose without, glabrous within. Flowering stems scapose, erect (1.5–)6.1–13.3(–17) cm long, white tomentose, becoming glabrate at maturity. Inflorescences umbellate. Bracts mostly semifoliaceous, 2–4(–6), narrowly oblong to narrowly elliptic, 2–5 mm long, 1–2 mm wide, white tomentose. Peduncles slender, slightly spreading, (1.5–)2–8.5(–9.5) cm long, silky tomentose to glabrate at maturity, occasionally some peduncles have an extra whorl of bracts midlength. Involucres solitary, broadly campanulate, the tube 2–3 mm long, (2–)3–4(–5) mm wide, silky tomentose and densely glandular without, glabrous
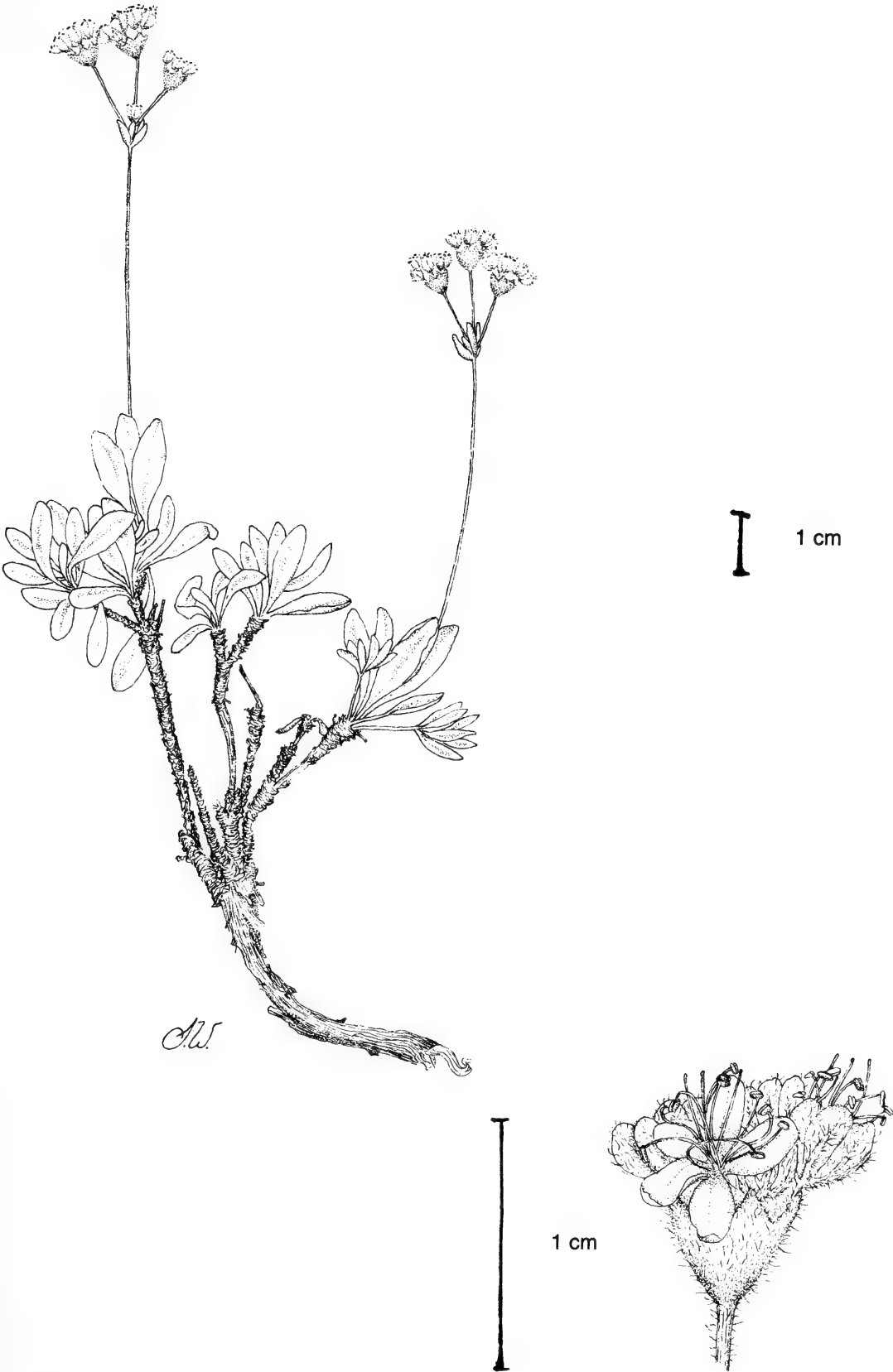
Fɪɢ. 1. *Eriogonum spectabile*. Left-habit. Right-involucre. Drawn from Corbin 906.

within; involucral teeth 5–7, acutely triangular, 1–1.2 mm long; bractlets numerous, linear, 2–3 mm long, fringed with long, silky hairs and minute gland-tipped cells. Pedicels 2.5–4 mm long, glabrous below, glandular and slightly hairy above. Flowers white (in anthesis) to pink or reddish (in fruit, also in bud). Stipe essentially lacking, 0.1–0.2 mm long. Tepals 6, with slightly darker greenish to reddish bases and midribs (midribs greenish within and dark pink without), 4–6 mm long (mostly 4–4.5 mm in flower, longer in fruit), densely hairy without with long, slender, silky-white hairs and short, capitate glands, essentially glabrous within except for minute glands and some hairs mainly along the midrib; tepals essentially similar, obovate, those of the inner whorl slightly longer than the outer whorl, united for less than ¼ of their length. Stamens ? included to exerted, 2.5–3(–6.5) mm long, the filaments sparsely pilose at the base; anthers red when fresh, purplish-red to purple when dried, 0.6–0.7 mm long, broadly ovate. Gynoccium with a style 1–1.3(–1.5) mm long. Achenes light brown, 3–4 mm long, tomentose, the subglobose base tapering to a stout, 3-angled beak.

Paratypes. Topotypes—30 Jul 1997, *Barron s.n.* (Lassen National Forest herbarium), 18 Aug 1997, *Barron s.n.* (CHSC, JEPS, MARY, Lassen National Forest herbarium), 8 Sep 1997, *Corbin et al. 861* (MARY), 8 Aug 1998 *Corbin et al. 906* (Lassen National Forest herbarium). USA, California: Plumas Co., ca. 2.2 km SW of Hay Meadows trailhead to the Caribou Wilderness, T30N, R7E, sect. 28 SW ¼ of SW ¼, MDM, 23 Sep 1997 *Corbin 882* (MARY, Lassen National Forest herbarium); ca. 2.2 km WSW of Hay Meadows trailhead, T30N, R7E, sect. 28 NW ¼ of SW ¼, MDM, 23 Sept 1997 *Barron s.n.* (Lassen National Forest herbarium).

Eriogonum spectabile is most closely related to *E. pendulum* S. Watson; both are members of an as yet undescribed section of the subg. *Eucycla* (Nutt.) Kuntze. The new species is a shorter, more compact plant than *E. pendulum* with more numerous branches at the base, narrower leaves with the pubescence equally distributed on both surfaces, longer petioles, reduced umbellate inflorescences, broadly campanulate involucres, and densely pubescent flowers with gland-tipped hairs among the silky-white ones. *Eriogonum pendulum* is found in extreme northwestern California (Del Norte Co.) and adjacent southwestern Oregon (Josephine Co.) in dry sandy soil in mixed evergreen forests not unlike that of *E. spectabile* (see below). The specific epithet refers to the spectacular appearance of this small shrub, which is quite attractive. We suggest the common name "Barron's buckwheat" to acknowledge the first collector.

Eriogonum spectabile appears to be limited to three small occurrences, all within one quarter section. The first discovered occurrence (and the type locality) is the largest; 194 plants were counted on

8 Sep 1997. The second occurrence had 54 plants on 23 Sep 1997, and the third only three (also on 23 Sep 1997). Numbers were similar in 1998 and 1999 visits. All known locations are on the Lassen National Forest in northeastern California within about 5 km of Lassen Volcanic National Park, and about 1.2 km from the Forest's Caribou Wilderness Area. This region is considered part of the southern limit of the Cascades Range. Extensive searches in adjacent Lassen National Forest areas were made in 1997, 1998, and 1999. Lassen Volcanic National Park has been fairly well botanized in the past (Oswald et al. 1995, Gillett et al. 1961), but no collections from Lassen Volcanic National Park are known. The Caribou Wilderness Area contains extensive apparently suitable habitat, much of which has not been surveyed, so *Eriogonum spectabile* may occur there as well.

The new species grows in open areas on minor ridges within a *Pinus contorta* Loudon. subsp. *murrayana* (Grev. & Balf.) Critchf., *Abies magnifica* Andr. Murray var. *magnifica,* and *A. concolor* (Gordon & Glend.) Lindley forest, at 2010 to 2025 m elevation. The general area is Quaternary glacial deposits (Lydon et al. 1976), with moraines forming low ridges interspersed by several small kettle lakes. Glaciation is particularly evident at the type locality, as shown by glaciated andesite bedrock or large boulders with smooth and striated surfaces, and chatter marks on the larger surfaces.

Arctostaphylos nevadensis A. Gray, which is abundant in this general area, is the species most closely associated with *Eriogonum spectabile*; however, *E. spectabile* occurs only in the less common openings between individuals of *Arctostaphylos nevadensis*. Other less abundant associates include *Achnatherum occidentale* (Thurbes) Barkworth subsp. *californicum* (Merr. & Burtt Davy) Barkworth, *Arctostaphylos patula* E. Greene, *Ceanothus prostratus* Benth., *Cymopterus terebinthinus* (Hook.) M. E. Jones var. *californicus* (J. Coulter & Rose) Jepson, and *Helianthella californica* DC. var. *nevadensis* (Greene) Jeps. The area receives about 60 inches (150 cm) of precipitation per year, mostly as snow (Ranz 1969).

Plants were in late flower on 30 Jul 1997 and 18 Aug 1997 visits, and in fruit in early Sep 1997. The spring of 1998 was much colder. The site was snow-covered on 17 Jun 1998; the plants were mostly vegetative on 22 Jul 1998, in bud on 8 Aug 1998, and in full bloom on 18 Aug 1998. Plants were in full flower on 26 Jul 1999, and still flowering and in early fruit on 31 Aug 1999.

At all three occurrences, most individuals appeared to be mature shrubs, and many had dead wood about the base. Few seedlings (only four at the largest occurrence in 1998, and none at the smallest) or apparently young plants were observed. Not all plants at an occurrence flowered: only 18 percent of the second occurrence flowered in 1997, but 60 percent of the adult plants at the

type locality flowered in 1998. The apparent low rate of recruitment may indicate an uncertain future for this species.

Although *Eriogonum spectabile* occurs relatively close to a wilderness area and national park, it is on national forest land without special designation. No human disturbance was observed at the three sites where the plant was found, but adjacent areas have been logged extensively. Firewood cutting is also common and numerous skid trails and wood-cutter roads criss-cross the general area. Besides potential human impacts, the low numbers and limited distribution of *E. spectabile* suggest it is at risk of extinction from natural habitat changes. One change may be an increase in competing vegetation (particularly *Arctostaphylos nevadensis,* but also other shrubs and the coniferous overstory), perhaps due to climate change and/or a change in the fire regime. Wildfire effects are not certain; given the plant's shrubby, presumably non-sprouting, long-lived growth form, it is likely that fire would kill existing plants. The species would then depend on seedling recruitment from the soil seed bank (of which we have no information) or from seeding in from adjacent areas, which is highly unlikely given its rarity and lack of obvious seed dispersal mechanism(s).

Another potential effect is browsing of flowering stems. On a 30 Sep 1998 visit to the second occurrence, nearly all flowering stems and some of the tips of the leafy shoots had been browsed, presumably by deer. The result is a virtual lack of intact seeds produced from this occurrence in 1998.

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NOTEWORTHY COLLECTIONS

ARIZONA

HEXALECTRIS REVOLUTA Correll (ORCHIDACEAE).—
Pima County, Baboquivari Canyon, and McCleary Canyon; Santa Cruz County, Sawmill Canyon. Between 1371 and 1524 meters elevation in canyon bottoms and sides of canyons, under oaks and mesquite, in association with Arizona walnut.

Previous knowledge. Previously known range was limited to portions of northern Mexico, and the Big Bend area of Texas. Voucher specimens of *H. revoluta* deposited at the University of Arizona Herbarium (ARIZ), Tucson, AZ collected in Baboquivari Canyon by Toolin in 1981 and McCleary Canyon by McLaughlin in 1986 were originally identified as *H. spicata*. Studies of fresh material in the field by the author indicated the plants are correctly *H. revoluta*.

Significance. First record of this species in Arizona, and represents a western range extension of approximately 290 miles (483 km) and a northern range extension of approximately 210 miles (350 km) from Big Bend National Park. Not known from New Mexico. *Hexalectris revoluta* is not currently a candidate for Federal Endangered Species status, but should be considered for listing due to rareness across its range. The McCleary Canyon location was recently included within the boundaries of land being considered for trade from the Forest Service to a mining developer. That trade is not currently under consideration.

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CALIFORNIA

ESCHSCHOLZIA RHOMBIPETALA E. Greene (PAPAVERACEAE).—Alameda County: Lawrence Livermore National Laboratory, Site 300, T3S R4E, SW ¼ Sec. 29, elev. 850 ft, on N-facing crumbling clay bank, with *Poa secunda* J. S. Presl, *Bromus madritensis* L. subsp. *rubens* (L.) Husnot, *Avena barbata* Link, *Stylomecon heterophylla* (Benth.) G. C. Taylor, *Microseris douglasii* (DC.) Schultz-Bip., *Blepharizonia plumosa* (Kellogg) E. Greene, 06 May 1997, *R. E. Preston 1028* (DAV).

Previous knowledge. Historically known from the interior foothills of the Hamilton and Diablo Ranges, with disjunct occurrences on the Carrizo Plains (W. Ernst, Madroño 17:281–294, 1964). Believed extinct (M. Skinner and B. Pavlik, Inventory of Rare and Endangered Vascular Plants of California, 1994) until rediscovered at Carrizo Plains in 1993 by David Keil and in 1995 by Curtis Clark (C. Clark, The genus *Eschscholzia:* California poppies and their relatives, http://www.intranet.csupomona.edu/~jcclark/poppy/, 2000).

Significance. First east Bay Area record since 1949. Site 300 is near Corral Hollow, where the species was last collected by Peter Raven. Subsequent attempts by Raven and Clark to relocate the Corral Hollow occurrences were unsuccessful (California Natural Diversity Database, Rarefind 2, Version 2.1.2, March 24, 2000 update; C. Clark, personal communication). Because the plants are small, they may be easy to overlook, and the plants may only

appear in favorable years (C. Clark, personal communication).

TRICHOCORONIS WRIGHTII (A. Gray) A. Gray (ASTERACEAE).—Merced County: Merced National Wildlife Refuge, S of Mariposa Bypass, T9S, R12E, SW ¼ Sec. 3, elev. 100 ft, 21 May 1997, *R. E. Preston 1031* (DAV. CAS).

Previous knowledge. Native to Mexico, Texas. In California, known from four occurrences in Riverside County and four scattered locations in the Central Valley. California populations are presumed to be introductions (A. M. Powell *in* J. C. Hickman [ed.], The Jepson Manual: Higher Plants of California, 1993), although Skinner & Pavlik (1994) suggest that the species may be native to California. Previously thought to be extirpated in the Central Valley (Skinner and Pavlik 1994).

Significance. First Central Valley record since 1953. Found growing in the bypass floodplain, with *Eleocharis macrostachya* Britton, *Xanthium strumarium* L., *Malvella leprosa* (Ortega) Krapov., *Phyla nodiflora* (L.) E. Greene, *Polygonum arenastrum* Boreau, and *Frankenia salina* (Molina) I. M. Johnston.

SENECIO APHANACTIS E. Greene (ASTERACEAE).—Alameda County: Corral Hollow, 0.5 mi NW of Tesla town site, T3S R3E, SE ¼ of NE ¼ S26, elev. 1500 ft, scattered on barrens, with *Plantago erecta* E. Morris, *Bromus madritensis* L. subsp. *rubens* (L.) Husnot, *Erodium cicutarium* (L.) L'Hés, *Hypochaeris glabra* L., *Erodium botrys* (Cav.) Bertol., *Medicago polymorpha, Avena fatua* L., 21 April 1998, *Robert E. Preston 1097* (DAV, CAS).

Previous knowledge. Widely but infrequently collected in the California Coast Ranges south of San Francisco Bay; the Transverse Ranges; southwest California, including Santa Cruz Island; and Baja California. This species is included in list 1B of the CNPS Inventory (Skinner and Pavlik 1994).

Significance. First record for Alameda County and first San Francisco Bay Area collection since 1933. In the Jepson Manual, this species is reported to occur on drying alkali flats (T. M. Barkley *in* Hickman, 1993). However, information obtained from herbarium specimens indicates that it occurs on various substrates: clay; coarse sand; rock outcrops, including serpentinite; and soils with high gypsum content or high alkalinity. Common to all occurrences is a conspicuous absence of vegetative cover.

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CALIFORNIA

BOEHMERIA CYLINDRICA (L.) Sw. (URTICACEAE).—
Sacramento Co., widely scattered colonies in riparian zone along both sides of Georgiana Slough separating Andrus and Tyler Islands, from approx. 2 mi SW of Georgiana slough divergence from Sacramento River to approx. 11 mi along the slough to near The Oxbow; less common in Snodgrass Slough immediately upstream off the Sacramento River. Elev. ~ sea level. *G. F. Hrusa 14879, J. A. Hart,* 11 Oct. 1998, 2 mi SW divergence of Georgiana

Slough from Sacramento River on W side. Rhizomatous colony in opening at waters edge at or slightly below high tide level, also in shade beneath adjacent *Alnus rhombifolia* Nutt. 38°07'50.4"N; 121°34'55.6"W (CDA and to be distributed.); *G. F. Hrusa 15277, J. A. Hart, M. J. Hooper,* 24 Nov. 1999. Snodgrass Slough at Delta Meadows State Park, on exposed and partially submerged logs. Elev. ~ sea level. (CDA).

Previous knowledge. Native throughout the region east of the Rocky Mountains occurring in bogs, marshes and other wet places. Collected in Arizona near the turn of the century but only recently redocumented there (J. Boufford, Ariz-Nevada Acad. Sci. 26:42–43, 1992).

Significance. First records for California. In addition to the collected sites listed above, the species has been observed near the town of Rio Vista on the Sacramento River. It is assumed here that *Boehmeria cylindrica* is introduced to California, based primarily on its general occupation of disturbed and rip-rapped riverbanks. Moreover, the heavy boat traffic throughout the Delta region would appear to provide ample opportunity for introduction and spread of this species; however, it has also been found growing in less disturbed conditions and it may be a previously overlooked native opportunistically occupying disturbed situations.

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CALIFORNIA

ERYNGIUM CONSTANCEI Y. Sheikh (APIACEAE).—Sonoma Co., dense populations in two seasonal pools, one draining into the other, on summit of Diamond Mtn. 4 km SSW of the town of Calistoga. Elev. 685 meters, 38°32'30"N; 122°35'00"W. *G. F. Hrusa 13582a* (lower pool center), *13582b* (lower pool periphery), and *13582c* (upper pool), *A. Buckmann.* Oct. 05, 1996. Verified by L. Constance, November 1997. (CDA, UC/JEPS and to be distributed).

Previous knowledge. Previously known only from two sites, one the type locality, at and near Loch Lomond in Lake Co., approx. 35 km NNE. Described in 1983 (L. Sheikh, Madroño 30:93–101, 1983).

Significance. First record for Sonoma Co. Two sites are known near Loch Lomond in Lake County; the type locality immediately N of the Loch Lomond townsite and a second approximately 3 km to the east. The habitat on Diamond Mtn. appears similar to that at the type locality, but is dominated by *Quercus garryana* Hook., *Q. lobata* Nee and *Pseudotsuga menziesii* (Mirbel) Franco rather than the *Pinus ponderosa* Laws., *Quercus kelloggii* Newb. mix at Loch Lomond. The Diamond Mtn. pools have been variously disturbed, and apparently a permanent spring which in past times fed both pools was closed some decades before the current owners took up residence. How this affected the local hydrology and flora is unknown. The plants at Diamond Mtn. do not match exactly the form at the type locality, the divergence most noticeable in the larger number of flowers per capitulum and the variable habit, ranging from slender and upright on the pool margins, to prostrate and stout in the deepest center

of the lower pool. These and other similar populations in the Sonoma-Lake County region are currently under study to assess their relationship to both *E. constancei* and *E. aristulatum* Jepson.

The type locality is currently listed in Title 14 of the Fish & Game Code as the Loch Lomond Vernal Pool Ecological Reserve. At present such safety cannot be claimed for the Diamond Mtn. locality as the pools are in an area under active viticulture development and forest harvest. However, the current landowners are aware of the pools' botanical importance in addition to DFG and California Department of Forestry regulations concerning their protection. DFG plans to pursue some form of permanent protection.

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CALIFORNIA

ONONIS ALOPECUROIDES L. (FABACEAE).—San Luis Obispo Co., Temettate Rd. approx. 1 km by road NW of intersection with Suey Creek Rd., in NW corner of S6, T11N; R33W, SB meridian. 35°03'58.2"N; 120°23'59.9"W. Elev. 380 m. Occupying approximately ½ acre in open grazed woodland-savanna among *Quercus agrifolia* Nee, *Pinus sabiniana* Douglas, extending eastward down a dry arroyo to edge of riparian zone. *Perez & Parks s.n.,* 9 July 1998 (CDA), *Hrusa 14732 a–g,* 21 July 1998 (CDA and to be distributed). *Hrusa 14732c, 14732d, and 14732h* confirmed by R. B. Ivimey Cook (EXR) & S. Jury (RNG).

Previous knowledge. Native to southwest Europe, North Africa. Adventive in central Europe.

Significance. First record for North America. The propagule source(s) is unknown. First noticed by the landowner 2 years previous, the population apparently expanded rapidly into a dense but currently still more or less localized colony. In 1998 it was found spreading downslope along a dry drainage leading to Suey Creek and so may be expected more widely, at least locally, in the near future. The plants are unpalatable to the horses and burros that graze through the local area and because the species may form a dense stand capable of excluding more palatable vegetation it is currently the target of active eradication efforts by the San Luis Obispo County Agricultural Commissioners office. As of July 2000, an intensive outreach program to local residents by the Ag. Commissioners office has not revealed additional populations; however, the current one remains active.

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CALIFORNIA

AMBROSIA PUMILA (Nutt.) A. Gray (ASTERACEAE).—Riverside Co., Riverside, moist area along Arlington Avenue, La Sierra Heights, 26 Aug 1940, *Ruth Cooper s.n.* (Riverside Community College Herbarium); Nichols Road wetlands area, northwest of Nichols Road and west of

Alberhill Creek, southwest of the I-15 Freeway, Lake El-sinore 7.5′ Quad., T5S R5W NW/4 S25, alt. 384 m, ca. 1300 plants in Arbuckle loam soil, annual grassland with *Vulpia myuros* (L.) C. Gmelin, *Isocoma menziesii* (Hook. & Arn.) G. Nesom, *Nassella pulchra, Bromus rubens, Erodium botrys* (Cav.) Bertol., *Hirschfeldia incana* (L.) Lagr.-Fossat, *Hemizonia paniculata* A. Gray, and *Avena fatua* L., 18 Jul 1997, *D. Bramlet 2575* (UCR); Warm Springs Valley, Nichols road, 0.3 km by road W junction I-15 near head of Walker Canyon, ca. 2.8 km NW Lake Elsinore, alt. 383 m, 29 Jun 1997, *Fred M. Roberts Jr. 5043* (RSA); Warm Springs Valley, NW of Lake Elsinore, about Alberhill Creek at the head of Walker Canyon near Durant Siding, SE base of Alberhill Mountain, along Nichols Road, 0.2 miles SW of junction with Collier Avenue, near 33°42′N, 117°21′W, T5N R5W NW ¼ S25, alt. 381 m, 22 Jul 1997, *Steve Boyd 10017* (RSA).

Previous knowledge. Reported only from San Diego County by The Jepson Manual (J. C. Hickman, ed., 1993, U.C. Press) and from "sw San Diego Co." by Munz (A California Flora, 1959, U.C. Press) but a locality at Skunk Hollow, Riverside County is also known (Madroño, 1992, 39(2):157). This species is considered rare and endangered and is reported to be declining by the CNPS Inventory of Rare and Endangered Vascular Plants of California (Skinner and Pavlik, 1994, CNPS Inventory of Rare and Endangered Vascular Plants of California, 5th Ed.).

Significance. These specimens provide second and third localities for Riverside County and range extensions of 27 km WNW and 53 km NW from the previously reported site at Skunk Hollow. The La Sierra Heights plants, only now being reported 60 years after their collection, were from the wet alkaline areas that formerly existed from near the intersection of Arlington Ave. and Van Buren Blvd., and the Riverside Airport, to the vicinity of California Ave. at Jackson Street. Unfortunately, there is little chance the plants persist there as the area is now largely paved and urbanized, though a few small pockets of marginal habitat do remain. The record at RCC was represented by three replicate specimens! It is unfortunate that two of these were not distributed to larger herbaria where they would have more rapidly come to the attention of the botanical community. Perhaps something could have been done to salvage part of this population if the location had been generally known. The Nichols Road population is under considerable threat due to its location in a rapidly urbanizing area. These discoveries highlight both the need to look for this species in other moist alkaline places in western Riverside County and the importance of checking small and inactive herbaria for significant records of other rare plants.

Dicoria canescens A. Gray (ASTERACEAE).—San Bernardino Co., Rialto [actually Colton, near the city boundary], degraded sand dunes on Slover Ave. just E of the tank farms and E of Riverside Ave., S of I-10 Freeway, very common, 14 Oct. 1993, *Chet McGaugh s.n.* (UCR); same location, 34°04′N, 117°22′W, alt. 320 m, ca. 200 plants seen in loose blowsand at summit of dune, in and near a disturbed OHV area, very local at this site and at another ca. 700 m further west, 14 Sept. 1999, *A. C. Sanders, S. Boyd and M. Provance 23073* (RSA, UCR).

Previous knowledge. A native plant of desert dunes, previously unrecorded on the coastal slope of California, except as a waif along the railroad near Elysian Park in Los Angeles (*A. Davidson s.n.* in 1892 and 1893, POM; H. M. Hall, Compositae of Southern California, Univ. of California Publ. Botany, Vol. 3, 1907).

Significance. First records of the species in natural habitat west of the deserts and a range extension of 55 km WNW from the Cabazon area. The species is well established at this site, which is a remnant of the formerly extensive Colton Dunes. We cannot be certain that the species was not introduced, but it appears native and is present in an arid interior valley in the best available natural habitat on the coastal slope. It is surprising that this species has so long escaped detection if it is native at this site, but other typically desert species are also found nearby, including *Camissonia campestris* (E. Greene) Raven, *Encelia farinosa* Torrey & A. Gray, *Eriophyllum wallacei* (A. Gray) A. Gray, *Malacothrix glabrata* A. Gray, and *Prosopis glandulosa* Torrey. While this area has long had an active botanical community, the total number of collectors has never been great, and it's probable that the dunes have just not been thoroughly surveyed in the fall, when few other plants are flowering.

Erodium malacoides (L.) Willd. (GERANIACEAE).— San Bernardino Co., Blue Mtn., Grand Terrace, 34°01′14″N, 117°18′14″W, alt. 396 m, abundant on the pediment near a water tank on the W side of the mountain, associated with *Heterotheca grandiflora* Nutt., 4 Apr 1998, *M. C. Provance 350* (UCR).

Previous knowledge. Weed introduced from Europe. Previously reported in California only from the northern San Joaquin Valley and San Francisco Bay areas.

Significance. First record for San Bernardino County and southern California and a range extension of over 600 km from the San Francisco Bay region. This weed should be sought in other areas in southern California and its status and spread carefully monitored.

Koeleria phleoides (Villars) Pers. (POACEAE).—Riverside Co., Jurupa Mtns., Sunnyslope near Rattlesnake Mtn., Armstrong St., 0.1 mi. south of San Bernardino Co. line, 34°01′59″N, 117°24′53″W, T2S R5W NW/4 S4, alt. 1050 ft, in hard dry soil in a disturbed field, 7 Mar 1998, *M. C. Provance 174* (ARIZ, UCR). Det. by J. & C. Reeder, 1999.

Previous knowledge. Uncommon introduction, reported from scattered locations from Santa Barbara and Kern Counties through northern California.

Significance. First record for Riverside County and a range extension of 250 km southeast from Santa Barbara County.

Monardella pringlei A. Gray (LAMIACEAE).—San Bernardino Co., sand hills west of Colton, 17 May 1941, *J. C. Roos 2472* (La Sierra College Herbarium).

Previous knowledge. This species, a very local endemic of the Colton Dunes, has generally been thought extinct since 1921 (Skinner and Pavlik, 1994).

Significance. This collection extends the known chronological range of this species by 20 years, but unfortunately we still have no evidence that the species has persisted until today. Like the *Ambrosia* record above, this record emphasizes the need to examine *all* herbaria for informative collections. This population was reported on the label to have been "mutilated by grasshoppers", though the specimen preserved was not too badly damaged. The recent discovery of other noteworthy species on the remnants of the Colton Dunes offers hope that this species may yet be rediscovered.

Nama stenocarpum Gray. (HYDROPHYLLACEAE).— Orange Co., San Joaquin Hills, Emerald Canyon, 3 km up canyon from Pacific Coast Highway, 2.75 km SW of intersection of Laguna Canyon Rd. and El Toro Rd., Laguna

Beach, 33°34′25″N, 117°47′10″W, a few plants on sandbar in steep incised channel with *Typha* sp., *Chenopodium ambrosioides* L., *Juncus xiphoides* E. Meyer and *Baccharis salicifolia* (Ruíz Lopez & Pavón) Pers., alt. 122 m, 21 July 1998, *A. L. Wolf 402* (UCR); Laguna Lakes (northernmost lake), W of Laguna Canyon Rd., Laguna Beach, 33°36′50″N, 117°45′30″W, alt. 118 m, 30+ plants on south edge of lake on drying margin with *Petunia parviflora* A. L. Juss., *Rorippa curvisiliqua* (Hook.) Britten and *Lythrum californicum* Torrey & A. Gray, 26 June 1998, *A. L. Wolf 358* (UCR); Lambert Reservoir, N of El Toro Marine Corps Air Station, 33°41′32″N, 117°42′40″W; alt. 134 m, few plants on mudflat on S edge of reservoir with *Ammania robusta* Heer & Regel, *Lythrum hyssopifolium* L., and *Juncus bufonius* L., 15 May 1998, *A. L. Wolf 276* (UCR); Peters Canyon Channel, E side of channel between Alton Pkwy and Barranca Pkwy, Tustin, 33°41′30″N, 117°49′17″; alt. 15 m, 2 plants in sediment basin adjacent to channel in the southwest portion of recently bladed field, 1 July 1998, *A. L. Wolf 414* (UCR); Riverside Co., Mystic (San Jacinto) Lake, 1.4 miles SE of Jackrabbit Trail on Gilman Springs Rd., 1.4 mi S of Glen Eden Hot Springs, 33°52′31′N, 117°03′W, alt. 433 m, common on receding lakeshore with numerous herbs, 26 Sep 1999, *A. C. Sanders & M. Provance 23120* (UCR, and to be distributed); same location, 15 Oct 1999, *A. C. Sanders, D. Bramlet, M. Costea & T. Salvato 23173* (UCR, and to be distributed).

Previous knowledge. A rare plant of seasonally moist areas from scattered counties, mainly coastal in southern California and extending south into Mexico. This species is considered rare in California but more or less common elsewhere (Skinner and Pavlik 1994). Not recorded on the mainland of southern California since 1939, nor anywhere in California since then, except for two collections on San Clemente Island (California Natural Diversity Database), the last in 1991.

Significance. First records for Riverside County and first records for California, except for San Clemente Island, in over 60 years. This rare plant is still a member of the mainland California flora.

QUERCUS PALMERI Engelm. (FAGACEAE).—Riverside Co., Jurupa Mountains, Rattlesnake Mt. near Crestmore Heights, ca. 4.2 km NW of downtown Riverside, 34°01.59′N, 117°23.81′W, T2S R5W S3, alt. 400 m, ca. 50 individual shrubs forming a dense and nearly homogenous vegetation over an area of approximately 25 m × 8 m, growing in a nook on a rocky north-facing slope, associated with *Prunus illicifolia* (Nutt.) Walp., *Ribes indecorum* Eastw. and *Phacelia ramosissima* Lehm., 14 Apr 1998, *Mitchell C. Provance 441* (UCR); Jurupa Mountains, Rattlesnake Mt. (hill 1452) above Crestmore, NW of Riverside, Fontana 7.5′ Quad., 34°02′N, 117°23.5′W, T2S R5W center of W/2 S3, alt. 365–400 m, dense colony in a notch on the ridge and in adjacent rocky gully between outcrops on the N-facing granitic slope, coastal sage scrub with chaparral elements, *Prunus illicifolia, Ribes indecorum, Eriogonum fasciculatum* (Benth.) Torrey & A. Gray, *Rhamnus crocea* Nutt., *Mimulus aurantiacus* Curtis, *Rhus trilobata* Torrey & A. Gray, *Salvia mellifera* E. Greene, *Toxicodendron diversilobum* (Torrey & A. Gray) E. Greene, etc., 14 May 1998, *A. C. Sanders and Mitch Provance 21848* (CAS, DAV, RSA, SD, UC, UCR).

Previous knowledge. Occurrences of this species are patchy from Colusa Co., California south to Baja California, Mexico and to the east in Arizona. In southern California, the species is most common in the Peninsular

Range, San Jacinto Mountains and south, but also occurs on the desert slopes of the San Gabriel and San Bernardino Mountains. There is a record of a single plant in the Little San Bernardino Mountains. This species has been considered for inclusion in the CNPS Inventory of Rare and Endangered Vascular Plants of California.

Significance. First known record of this species for the South Coast subregion (Hickman 1993) and a range extension of approximately 38 km SSW from the nearest known populations on the north side of the San Bernardino Mtns., near Mojave River Forks. This population is well separated from the other known populations, and occurs far below the lowest elevation previously known for the species in the region. The rate of sexual reproduction in this population appears to be extremely low, although some of the plants do appear to be making a few healthy acorns. It is amazing that this conspicuous species has escaped detection on the outskirts of a large city that has had an active botanical community for over 100 years. For example, some early botanists and plant collectors who were Riverside residents, prior to the establishment of UC Riverside, include: Charlotte M. Wilder (whose house was *in* the Jurupa Mtns.), Fred M. Reed, Harvey Monroe Hall, David D. Keck, and Edmund C. Jaeger. In addition, Samuel B. Parish's residence in San Bernardino was less than 15 km NE of the *Quercus palmeri* site. This discovery points up the need to continue searching for new species and important range extensions even in "well known" areas: an unexplored ridge can hide something new or interesting, and there are many unexplored ridges.

—MITCHELL C. PROVANCE and ANDREW C. SANDERS, Herbarium, Dept. of Botany & Plant Sciences, University of California, Riverside, CA 92521-0124, VALERIE SOZA and STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711, DAVID BRAMLET, 1691 Mesa Dr. A-2, Santa Ana, CA 92707 and ADRIAN L. WOLF, Harmsworth Associates, 36 Bluebird Lane, Aliso Viejo, CA 92656.

CALIFORNIA

All the following collections are from the San Bernardino Mountains.

BRICKELLIA KNAPPIANA Drew (ASTERACEAE).—San Bernardino Co., northeast side of Blackhawk Mountain, east of Blackhawk Canyon, 34°21′06″N 116°47′24″W, elev. 1372 m, shrub 1.8 m tall in alluvium of minor canyon, northeast-facing wash, 10 Aug 1998, *Valerie Soza et al. 409* (RSA, and to be distributed).

Previous knowledge. This probable hybrid (treated as a species in all available manuals) between *B. desertorum* Cov. and *B. multiflora* Kellogg is known from only a few locations in the northern and eastern mountain ranges of the Mojave Desert, almost always at sites where both parents are present. Previously collected from the Argus, Funeral, Panamint, and Kingston Mountains, but with the type locality at an undefined site along the Mojave River. The type locality is given simply as "in the neighborhood of the Mohave River" (*Pittonia,* 1888, 1:260). The vagueness of the collection data inspires little confidence that the site was particularly near the Mojave River, especially since the plant has not, in the 110 years since, been recorded there.

Significance. First record for the San Bernardino Moun-

tains, which extends the range of this taxon 90 km southward from the closest known locality in the Argus Range.

BRICKELLIA MULTIFLORA Kellogg (ASTERACEAE).—San Bernardino Co., canyon running from west to east along the northern edge of Horsethief Flat, 34°19.487′N 116°45.841′W, elev. 1372 m, rocky drainage area near mouth of canyon, seasonally moist, subjected to carbonate scree slides from along canyon walls, 29 Jun 1998, *Mitchell C. Provance & Valerie Soza 792* (UCR).

Previous knowledge. Uncommon shrub occurring from the northern and eastern Mojave Desert of California to Nevada, particularly in the mountains of Inyo County, the White Mountains of Mono County, at Little Lake in Kern County, and the Kingston, Clark and Granite Mountains of San Bernardino County.

Significance. First record for the San Bernardino Mountains, which extends the range of this species about 100 km southwestward from the nearest known occurrence in the Granite Mtns. near Kelso. It is noteworthy that this species turned up at about the same time that its hybrid progeny, *B. knappiana* Drew, was also discovered in the range. It is interesting that several species traditionally known from the northern and eastern Mojave Desert (e.g., *Baileya multiradiata* A. Gray, Madroño 43 (4):524, and the plants reported here) have recently been found on the northern slopes of the San Bernardino Mountains, as that area has begun to be explored away from the major routes of travel.

CAMISSONIA PTEROSPERMA (S. Watson) Raven (ONAGRACEAE).—San Bernardino Co., west of Horsethief Flat, above road 3N03A, 34°19′06″N 116°47′03″W, elev. 1768 m, scarce annual in open WNW-facing slope, 16 Jul 1998, *Valerie Soza & Tasha LaDoux 390* (RSA); San Bernardino Mountains, northwest of Tip Top Mountain, east of Arrastre Creek, 34°15′59″N 116°43′45″W, elev. 1920 m, rare annual on open rocky north-facing lower slope, 30 Jul 1998, *Valerie Soza & Tasha LaDoux 404* (RSA).

Previous knowledge. Rare annual in northern mountain ranges of the Mojave Desert, e.g., Panamint and Clark mountains, and Inyo and White mountains east to Last Chance Range and Fish Lake Valley, to Utah and Oregon.

Significance. First record for the San Bernardino Mountains, range extension of about 100 km southwestward from Clark Mountain.

CORNUS GLABRATA Benth. (CORNACEAE).—Riverside Co., Morongo Indian Reservation, very locally common at a seep along a gully at the west end of Burro Flat, 33°59′N, 116°52′W, alt. 1160 m, 14 Nov 1997, *A. C. Sanders & T. Tennant 21596* (DAV, RSA, SD, TEX, UC, UCR, UTC).

Previous knowledge. Scarce in southern California and known from Riverside County only from a single collection from the San Jacinto Mountains made in 1922 (P. A. Munz 5806, alt. 1500 m, Hemet Valley, frequent along banks of Pipe Creek) based on specimens at UCR and RSA.

Significance. First record for the San Bernardino Mountains, second record from Riverside County and the first collection of this species from that county in 77 years.

CYNANCHUM UTAHENSE (Engelm.) Woodson (ASCLEPIADACEAE).—San Bernardino Co., E. of Horsethief Flat, 0.5 km N of the Arrastre Creek Dam, 34°19.44′N 116°45.77′W, elev. 1433 m, on a steep, barren, sandy, SE-facing slope, 23 Jun 1998, *Mitchell C. Provance & Valerie Soza 744* (UCR).

Previous knowledge. Uncommon perennial occurring on the Mojave Desert of California and to Utah and Arizona.

Significance. First record for the San Bernardino Mountains and the Transverse Ranges and extends the range of this species slightly (10 km southwest) from the nearest known occurrence of Old Woman Spring on the southern Mojave Desert.

GLYCERIA OCCIDENTALIS (Piper) J. C. Nelson. (POACEAE).—Riverside Co., Morongo Indian Reservation, very locally common in mud around the sag pond at the southeast end of Burro Flat, 33°59.5′N, 116°51′W, T2S R1E SE/4 S14, alt. 1150 m, 24 Apr 1996, *A. C. Sanders & S. Hawkins 18088* (RSA, UCR, and to be distributed). Det. by Travis Columbus.

Previous knowledge. Northwestern California and north to Idaho and British Columbia, the furthest south previously known populations are apparently in San Mateo County (P. A. Munz, 1968, Supplement to A California Flora, University of California Press).

Significance. First record for southern California and a range extension of 650 km from the San Francisco Bay area. The site where this species was collected was a shallow but permanently wet sag pond on the San Andreas Fault from which, reportedly, peat was formerly harvested. This bizarre disjunction in the distribution of a native plant suggests that the species should be sought in other wet areas in central and southern California. Travis Columbus notes that this species is possibly not distinct from the Eurasian species *Glyceria declinata* Brébiss. That species has also been reported from northern California (e.g., A. S. Hitchcock and A. Chase, 1935, Manual of the Grasses of the United States; P. A. Munz, 1959, A California Flora, University of California Press), but is not mentioned in the Jepson Manual. *Glyceria declinata* was reported in the literature for California in 1957 by Beecher Crampton from Stanislaus County, south of Oakdale, further ESE from the San Francisco Bay area (Leaflets of Western Botany 8 (6):160).

NICOTIANA ACUMINATA Hook var. MULTIFLORA (Philippi) Reiche (SOLANACEAE).—Riverside Co., Morongo Indian Reservation, lower Hathaway Creek Cyn., 33°58′N, 116°52′W, elev. 838 m, disturbed roadside especially in moist areas, margins of riparian forest, 20 Aug 1998, *A. C. Sanders 22232* (UCR).

Previous knowledge. An introduced weed from South America, long known from northern California, but only first reported in southern California in 1996 from San Bernardino County (Madroño 43(2):334–336).

Significance. First record for Riverside County; extends its southern California range 18 km southeast from Mill Creek Cyn., and further documents the establishment and spread of this introduced weed in southern California.

—VALERIE SOZA, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711; MITCHELL C. PROVANCE and ANDREW C. SANDERS, Herbarium, Dept. of Botany & Plant Sciences, University of California, Riverside, CA 92521-0124; and STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

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COLORADO

ALICIELLA SEDIFOLIA (Brandegee) J. M. Porter [*Gilia sedifolia Brandegee*] (POLEMONIACEAE).—Hinsdale Co.,

San Juan Mts., Half Peak; 19 km SW of Lake City, T42N R6W SEC25 SE¼; 4110 m. South facing slope, gravelly patches with no other vegetation, common locally. 5 August 1995, *Susan Komarek* 478 (COLO 457147).

Previous knowledge. Evidently a rare endemic; thought extinct since original collection by Purpus in 1893 [Gunnison County, Uncompahgre Range, Sheep Mt., 11,800′, July 1893. Purpus 697 (GH)].

Significance. First collection in 103 years.

ASCLEPIAS INVOLUCRATA Engelmann *ex* Torrey (ASCLEPIADACEAE).—Bent Co., 18 km NE of Las Animas, T21S R51W SEC23 NW¼; 1260 m. Transitional zone between shortgrass and sandsage prairie, with *Buchloë dactyloides, Psoralidium tenuiflorum,* and *Oligosporus filifolius.* 7 June 1998, *Dina Clark* 686 (COLO 471324).

Previous knowledge. Southern Great Plains, New Mexico, Arizona, and Mexico; one collection from Las Animas County, Colorado in 1948 [Rogers 5834, May 31, 1948. (COLO 55248)] (Great Plains Flora Association, Flora of the Great Plains 1986).

Significance. First Colorado collection in 50 years. The documented distribution of this species may become better known with increased field work in the eastern part of the state.

ASTROLEPIS INTEGERRIMA (Hooker) Benham & Windham (PTERIDACEAE).—Las Animas Co., Mesa de Maya, Jesus Mesa, near Colorado - New Mexico State Line, ca. 85 km ESE of Trinidad; T35S R54W SEC16 NE¼; 1540 m. Dry, southwest facing slope in crevice of Dakota sandstone outcrop. 19 September 1994, *Dina Clark* 582 & Carolyn Crawford (COLO 455480).

Previous knowledge. Arizona, Nevada, New Mexico, Oklahoma, Texas, and Mexico (Great Plains Flora Association, Flora of the Great Plains 1986).

Significance. First Colorado record. Apparently the northernmost record of this New World genus (Flora of North America Association, Flora of North America Vol. 2 1993).

BOTHRIOCHLOA SPRINGFIELDII (Gould) Parodi [*Andropogon springfieldii* Gould] (POACEAE).—Las Animas Co., Mesa de Maya, vicinity of upper Gotera Canyon, ca. 70 km ESE of Trinidad; T34S R55W SEC27 SE¼; 1700 m. South facing slope in grassy breaks. 5 July 1993, *Dina Clark* 204 & C. Deihl (COLO 455362); 4 August 1993, *Dina Clark* 216 & P. Deihl (COLO 455213).

Previous knowledge. West Texas to Arizona (Great Plains Flora Association, Flora of the Great Plains 1986).

Significance. First Colorado record. A range extension of ca. 100 km and the northernmost record for this species (Great Plains Flora Association, Atlas of the Flora of the Great Plains 1977).

CHENOPODIUM CYCLOIDES Nelson (CHENOPODIACEAE).—Weld Co., ca. 25 km ENE of Greeley; T6N R63W SEC34 SE¼; 1430 m. *Andropogon hallii-Calamovilfa longifolia* grassland on eolian deposited sand. 3 September 1997, *Dina Clark* 634 (COLO 469818).

Previous knowledge. Southwest Kansas south through west Texas, west to southern New Mexico; known in Colorado from Las Animas and Pueblo counties (Spackman et al., Colorado Rare Plant Field Guide 1997).

Significance. Northward range extension of ca. 250 km for this rare, or perhaps overlooked, species.

DIPLACHNE DUBIA (Kunth) Scribner [*Leptochloa dubia* Humboldt, Bonpland, & Kunth] (POACEAE).—Las Animas Co., Mesa de Maya, ca. 115 km E of Trinidad; T33S

R51W SEC25 SE¼; 1450 m. Bottom of dry, rocky, S facing slope. 4 September 1993, *Dina Clark* 283, T. Hogan, & R. Brune (COLO 455445).

Previous knowledge. Texas, western Oklahoma, Arizona, and Mexico; also south Florida and Argentina (Correll and Johnston, Manual of the Vascular Plants of Texas 1970).

Significance. First Colorado record. A range extension of ca. 500 km from previously known location (Neil Snow personal communication).

ELEOCHARIS XYRIDIFORMIS (Fernald) Brackett (CYPERACEAE).—Logan Co., Vicinity of Sterling, Peetz Table, 40°56′36″N, 103°10′19″W; 1300 m. Low swale, on clay-sand substrate. 31 August 1997, *W. A. Weber* 19273 & Ron Wittmann (COLO 467546). Cheyenne Co., Three km E of Kit Carson on Hwy 40; 1250 m. Low swale in sand hills of high plains. 7 September 1997, *W. A. Weber* 19382, Ron Wittmann, & Dina Clark (COLO 467358).

Previous knowledge. North Dakota and Montana, south to Texas and Mexico (Great Plains Flora Association, Flora of the Great Plains 1986).

Significance. First Colorado record. Probably overlooked previously, and to be expected more frequently with increasing field work in eastern Colorado.

FESTUCA SUBULATA Trin. (POACEAE).—Rio Blanco Co., North Fork of White River near North Fork Campground, White River N.F., ca. 20 km NE of Buford; T1N R90W SEC13; 2400 m. Riverbank with *Alnus incand* (L.) Moench and *Salix drummondiana* Hook. 9 August 1992, *Nan Lederer* 3661 (COLO 451683); 3 September 1992, Gwen Kittel (COLO 451607).

Previous knowledge. Alaska to Alberta, south to California, east to Idaho, Montana, Utah, and Wyoming. Reported from northern tiers of Utah (Welsh, A Utah Flora 1993) and Wyoming (Dorn, Vascular Plants of Wyoming 1992).

Significance. First Colorado record. Approaching the southern extent of its range in North America (known from the central Sierra Nevada of California).

HELENIUM MICROCEPHALUM De Candolle (ASTERACEAE).—Las Animas Co., Mesa de Maya, ca. 105 km E of Trinidad; T33S R51W SEC22 NW¼; 1500 m. Muddy edge of stock pond in shortgrass prairie. 16 September 1994, *Dina Clark* 554 (COLO 455583).

Previous knowledge. Southwest Oklahoma, Texas, southern New Mexico, to northern Mexico (Great Plains Flora Association, Flora of the Great Plains 1986).

Significance. First Colorado record. A species of the southern Great Plains, this record represents a range extension of nearly 300 km.

HETEROSPERMA PINNATUM Cavanilles (ASTERACEAE).—Las Animas Co., Mesa de Maya, ca. 75 km E of Trinidad; T34S R56W SEC20 NE¼; 1700 m. Among sandstone slabs near drainage; shortgrass prairie. 17 September 1994, *Dina Clark* 566 (COLO 455475).

Previous knowledge. Mexican highlands, north to Arizona and Texas (Correll and Johnston, Manual of the Vascular Plants of Texas 1970).

Significance. First Colorado record. A Chihuahuan species at its northernmost point in North America; an extension of its previously known range from Santa Fe County, New Mexico and the Davis Mountains of Texas.

REVERCHONIA ARENARIA Gray (EUPHORBIACEAE).—Bent Co., S shore of John Martin Reservoir; T23S R49W SEC17 SW¼ of NW¼; 1150 m. Sandsage prairie on dune.

6 June 1998, *Dina Clark* 683 (COLO 471323); 30 July 1998, *Dina Clark* 740 (COLO 471325).

Previous knowledge. Oklahoma, Kansas, Texas, New Mexico, Utah, Arizona, and northern Mexico (Great Plains Flora Association, Flora of the Great Plains 1986).

Significance. First Colorado record. Northernmost record for this species; a range extension of ca. 200 km.

TRITELEIA GRANDIFLORA Lindl. [*Brodiaea douglasii* Wats.] (ALLIACEAE).—Montezuma Co., Boggy Draw near Peel Reservoir; T38N R14W SEC7 SW¼; 2400 m. Pine-oak vegetation; population of about 2000 plants in 8 ha area. 22 June 1998, *Leslie Stewart* 4 (COLO 470260, 470261).

Previous knowledge. A showy species of the northwest; nearest reports from the Wasatch Range of northeast Utah (Welsh, A Utah Flora 1993) and northwestern Wyoming (Dorn, Vascular Plants of Wyoming 1992).

Significance. First Colorado record. There is some speculation this may have been transported by indigenous people as a food source. Specimen was collected by Charlotte Thompson, a seasonal employee of the U.S. Forest Service, in the process of clearing a timber sale. Population was reportedly protected from lumbering operation (Leslie Stewart personal communication).

—DINA CLARK and TIM HOGAN, University of Colorado Herbarium (COLO), Campus Box 350, Boulder, CO 80309.

OREGON

CAREX CHORDORRHIZA Ehrh. ex L. f. (CYPERACEAE).—Clatsop Co., weedy cranberry fields, with *C. arcta* Boott, W of Cullaby Lake, elev. 4 m, T7N R10W S22, 2 Oct 1999, *P. F. Zika 14455* WTU; Coos Co., well-established weed in cranberry fields, with *Vaccinium macrocarpon* Aiton, *Aster subspicatus, Lysimachia terrestris,* between Spruce Hollow and Coquille River, elev. <50 m, T28S R14W S20 E¼, 20 June 1997, *P. F. Zika 13217 & B. Wilson* (OSC, MICH); Curry Co., weed in cranberry fields, with *Agrostis exarata,* 2.5 km W of Route 101, SW of Floras Lake, elev. ca. 15 m, T31S R15W S20, 21 August 1997, *P. F. Zika 13365 & B. Wilson* (OSC).

Previous knowledge. Creeping sedge is a circumboreal sedge native in eastern and northern North America. The nearest native population is 380 km northeast in Okanogan Co., Washington (*Wooten 1334* WS).

Significance. First report for Oregon. All sites are associated with wetland cranberry agriculture, which began with the introduction of *Vaccinium macrocarpon* to Oregon in 1885. The cranberry vines are cut and hauled between farms to establish new cranberry fields. The process also transports weed seeds from one farm to the next. *Carex chordorrhiza* is known as a weed in cranberry fields in Wisconsin (Eck, The American Cranberry, 1990), where it is a native and invades from adjacent wetlands (A. A. Reznicek, personal communication). Creeping sedge is not reported as a weed from cranberry farms elsewhere in North America (Eck 1990). Thus we suspect *C. chordorrhiza* arrived in Oregon during the transport of cranberry vines from Wisconsin to Oregon. There are several other eastern native wetland plants that are reported below as new weeds in our area. All probably originated as propagules attached to cranberry vines transported from the eastern United States.

ESCALLONIA RUBRA (Ruíz & Pavón) Pers. (GROSSULARIACEAE).—Coos Co., naturalized weed on muddy shore and on disturbed ground in adjacent fields, with *Gaultheria shallon* Pursh, *Myrica californica* Cham., SE end of Lost Lake, NW of McTimmonds Road, elev. 7 m, T29S R15W S36 NW¼, 20 June 1997, *P. F. Zika 13207 & B. Wilson* (OSC).

Previous knowledge. Native to Chile. Commonly cultivated west of the Cascade Mts. in Oregon and Washington.

Significance. First report for Oregon as a garden escape. Naturalized in a wild setting in the New River Area of Critical Environmental Concern, Coos Bay District of the Bureau of Land Management.

FUCHSIA MAGELLANICA Lam. (ONAGRACEAE).—Coos Co., steep weedy roadside bank, with *Rubus armeniacus, Lathyrus latifolius* L., Route 101, Coos Bay, near North Bend town line, elev. ca. 10 m, T25S R13W S23, 18 June 1997, *P. F. Zika 13139 & B. Wilson* (OSC); Curry Co., weed in hedge rows, with *Rubus spectabilis* Pursh, *R. armeniacus, R. laciniatus* Willd., *Pseudotsuga menziesii* (Mirbel) Franco, near waste treatment plant, Wharf Street, Brookings, elev. ca. 20 m, T41S R13W S6, 19 May 1997, *P. F. Zika 13083* (WTU); roadside weed, Route 635 at 0.3 km NW of Yorke Creek, elev. 24 m, T37S R14W S18 NW¼ of SE¼; 19 June 1997, *P. F. Zika 13163, B. Wilson, & V. Stansell* (OSC).

Previous knowledge. Native to Chile and Argentina. Common ornamental in Oregon and Washington, occasionally fruiting west of the Cascade Mtns.

Significance. First report in Oregon as a garden escape. Most likely dispersed by fruit-eating birds.

HYPERICUM BOREALE (Britton) E. Bickn. (CLUSIACEAE).—Clatsop Co., weedy cranberry fields, W of Cullaby Lake, elev. 4 m, T7N R10W S22, 2 Oct 1999, *P. F. Zika 14449* OSC, WTU; Coos Co., common weed in moist sand, in and near cultivated cranberry fields, with *Vaccinium macrocarpon* Aiton, *Lysimachia terrestris, Juncus effusus,* Lower Fourmile Road, 1.5 km W of Route 101, elev. ca. 10 m, T30S R15W S1 NW¼ of NW¼, 20 August 1997, *P. F. Zika 13338, B. Rittenhouse, B. Newhouse, & B. Wilson* (OSC); sunny depression between cranberry fields, and nearby ditches, with *Sisyrinchium californicum* (Ker Gawler) Dryander, *Lotus corniculatus* L., *Rubus ursinus* Cham. & Schldl., *Panicum occidentale,* Croft Lake Road, 1.5 km W of Route 101, elev. ca. 15 m; T30S R15W S11; 20 August 1997, *P. F. Zika 13340, 13346* (OSC); Curry Co., cranberry fields and ditch margins, well established weed, with *Juncus bufonius* L., 2.5 km W of Route 101, SW of Floras Lake, elev. ca. 15 m, T31S R15W S20, 21 August 1997, *P. F. Zika 13367 & B. Wilson* (OSC).

Previous knowledge. Native to eastern North America, west to Illinois.

Significance. First record for Oregon. At present it appears to be restricted to cultivated cranberry fields, and adjacent moist, disturbed ground.

JUNCUS BREVICAUDATUS (Engelmann) Fernald (JUNCACEAE).—Clatsop Co., weedy cranberry fields, W of Cullaby Lake, elev. 4 m, T7N R10W S22, 2 Oct 1999, *P. F. Zika 14454* OSC, WTU; Curry Co., sandy banks near cranberry fields, with *J. bufonius* L., *J. canadensis, J. planifolius,* 2.5 km W of Route 101, SW of Floras Lake, elev. ca. 15 m, T31S R15W S20, 21 August 1997, *P. F. Zika 13366 & B. Wilson* (OSC).

Previous knowledge. Native to eastern North America, west to Minnesota.

Significance. First Oregon record. Another weed associated with cranberry agriculture.

JUNCUS CANADENSIS J. Gay ex Laharpe (JUNCACEAE).—Clatsop Co., weedy cranberry fields, W of Cullaby Lake, elev. 4 m, T7N R10W S22, 2 Oct 1999, *P. F. Zika 14452* OSC, WTU; Coos Co., mucky shoreline, with *Carex aquatilis* Wahlenb. var. *aquatilis, Dulichium, Lysimachia terrestris, Juncus supiniformis* Engelm., *Scirpus subterminalis* Torrey, Muddy Lake, elev. 5 m, T30S, R15W S11 SW¼, 20 August 1997, *P. F. Zika 13353 & B. Rittenhouse* (OSC); shallow water emergent, with *Potentilla palustris* (L.) Scop., *Gentiana sceptrum* Griseb., *Hypericum anagalloides* Cham. & Schldl., *Vaccinium macrocarpon* Aiton, E shore of unnamed pond, W of Lost Lake, elev. 7 m, T29S R15W S36 NW¼ of NW¼, 21 August 1997, *B. Newhouse 97055* (OSC); Curry Co., well established weed in ditches and cranberry fields, with *J. effusus* L., *J. falcatus* E. Meyer, *Scirpus setaceus* L., 2.5 km W of Route 101, SW of Floras Lake, elev. ca. 15 m, T31S R15W S20, 21 August 1997, *P. F. Zika 13360 & B. Wilson* (OSC).

Previous knowledge. Native to eastern North America, west to Minnesota. Reported as a weed in cranberry fields in New England (Sears et al., An Illustrated Guide to the Weeds of Cranberry Bogs in Southeastern New England, 1996).

Significance. First report for Oregon. Another weed associated with the cranberry industry. Our collections from undisturbed wetlands indicate this species is successfully invading native plant communities in southwestern Oregon.

JUNCUS PELOCARPUS E. Meyer (JUNCACEAE).—Coos Co., sandy soil in swamps and cranberry bogs, Bandon; 2 Sept 1958; *G. Scott s.n.* (OSC); sandy shoreline of irrigation pond, with *Lysimachia terrestris, Salix sitchensis* Bong., *Viola lanceolata,* near cranberry fields, Croft Lake Road, 1.5 km W of Route 101, elev. ca. 15 m; T30S R15W S11; 20 August 1997, *P. F. Zika 13339* (OSC).

Previous knowledge. Native to eastern North America, west to Minnesota. Noted as a weed in cranberry fields in New England (Sears et al. 1996).

Significance. First report for Oregon. Another weed associated with the water systems for cranberry farming.

SPIRAEA TOMENTOSA L. (ROSACEAE).—Coos Co., weed in cranberry fields, with *Vaccinium macrocarpon* Aiton, *Lysimachia terrestris, Aster subspicatus,* between Spruce Hollow and Coquille River, elev. <50 m, T28S R14W S20 E¼, 20 June 1997, *P. F. Zika 13213 & B. Wilson* (OSC).

Previous knowledge. Native to eastern North America, west to Minnesota. A weed in cranberry fields in New England (Sears et al. 1996).

Significance. First record for Oregon. Another weed associated with the cranberry industry.

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ALLOZYME DATA SUPPORT A EURASIAN ORIGIN FOR *CAREX VIRIDULA* SUBSP. *VIRIDULA* VAR. *VIRIDULA* (CYPERACEAE)

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Abstract

Carex viridula Michaux subsp. *viridula* var. *viridula* (Cyperaceae), the green sedge, occurs in wetland habitats distributed throughout northern and central North America. Its distribution also extends to the southern Rocky Mountain region in several disjunct sites, including alpine wetlands in Colorado, where it is rare. Populations of *C. viridula* from Colorado were investigated using starch gel electrophoresis of soluble enzymatic proteins coupled with substrate specific staining in order to describe genetic diversity and structure. The objective was to determine if Colorado populations exhibited the reduced genetic diversity expected of marginal populations when compared to other populations from North America and Europe. Genotypic data were collected for 15 enzyme systems encoded by 21 putative loci in 350 individuals from seven populations in Colorado and in 179 individuals from eight populations from elsewhere throughout the range in North America. Data from all North American populations were compared with data previously reported from European populations of this species by Bruederle and Jensen (1991). No variation, either within or among North American populations, was detected at any of the loci. However, North American populations were genetically differentiated from European populations, with significantly more diversity maintained by European populations. The surprising lack of genetic diversity in North American populations is probably the combined result of high levels of selfing and inbreeding, restricted ecological amplitude, and genetic drift. Genetic bottlenecks are presumed to have occurred as a result of climate changes associated with Pleistocene glaciation or founding events associated with colonization of North America by proposed ancestral European populations.

Since 1986, starch gel electrophoresis and allozyme analysis have been used to study genetic diversity in no fewer than 43 species representing nine sections of the genus *Carex*. These studies have been useful not only in elucidating systematic relationships (e.g., Whitkus 1992; Ford et al. 1998), but also in providing indirect estimates of mating systems (e.g., Waterway 1990), identifying hybrid origins (e.g., Standley 1990), and revealing correlations between genetic diversity and structure and certain life-history traits (e.g., Jonsson et al. 1996). However, few studies have examined genetic diversity in disjunct populations of a broadly distributed species of *Carex*.

Carex section *Ceratocystis* Dumort. (Cyperaceae) comprises seven species worldwide, which collectively occur throughout much of the northern hemisphere, particularly in boreal latitudes and the subalpine (Crins and Ball 1988). *Carex viridula* Michaux subsp. *viridula* var. *viridula*, the green sedge, is the only representative of section *Ceratocystis* in Colorado.

Carex viridula is putatively one of the most recently derived members of section *Ceratocystis*, although it is not entirely clear when it diverged from its closest relative, *C. viridula* subsp. *oedocarpa* (N.

J. Anderson) B. Schmid (Schmid 1984b; Crins and Ball 1989; Bruederle and Jensen 1991). It has been hypothesized that their common ancestor differentiated in West Europe. Thereafter, *C. viridula* is presumed to have colonized the remainder of the temperate and boreal northern hemisphere, perhaps before Pleistocene glaciation, by way of the Bering land bridge (Crins and Ball 1989).

Carex viridula is a short-lived perennial with a densely caespitose habit. It is monoecious, characterized by a single terminal staminate spike and several sessile pistillate spikes. It has been suggested that *C. viridula* is a dispersal generalist, with possible transport by biotic, e.g., birds and mammals, and abiotic agents, e.g., wind and water (Schmid 1984a; Crins and Ball 1989). While there are no apparent impediments to outcrossing, the breeding system is predominantly selfing. In a study by Schmid (1984a) examining the life history of *C. viridula*, tests for self-compatibility in the field and in experimental gardens using fine mesh bags to control pollination were positive. Additionally, inflorescences from which the staminate spike had been removed had maximum seed sets of only 10% when growing in the immediate vicinity of other fertile plants. Similarly, Bruederle and Jensen (1991) attributed low genetic diversity (e.g., proportion of polymorphic loci and observed heterozygosity) and deviations from Hardy-Weinberg equilibrium in West European populations of *C. viridula* to selfing. Genetic diversity was appor-

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tioned among populations with relatively little variation found within populations.

Ecologically, *C. viridula* is characterized by rapid growth and development, small stature, short life-span, early reproduction, large reproductive effort, and small population size (Schmid 1984a, b). As such, *C. viridula* is an early successional, *r*-selected species, or in Grime's (1979) classification, a ruderal species. Although *C. viridula* typically occupies moist, early successional sites characterized by fluctuating and unpredictable water levels, these can vary from calcareous, acidic, sandy, or organic shorelines; runnels in limestone barriers; wet meadows; marshes; on borders of streams, ponds, and lakes; and fens. This species' success in colonizing is likely due to its tolerance of diverse and fluctuating environments, high phenotypic plasticity, and ability to reproduce quickly and profusely (Schmid 1984a, b; Crins and Ball 1989).

Geographically, *C. viridula* is the most widespread taxon in section *Ceratocystis*, with a near circumboreal distribution. It is common throughout northern Europe, and much of northern and central North America; it is also scattered across the central and eastern parts of temperate Asia to the Pacific Ocean (Crins and Ball 1989). In North America, its range extends south in the Rocky Mountain region to several disjunct sites in Colorado, Wyoming, Utah, and Nevada. In the Southern Rocky Mountains, *C. viridula* occupies an uncommon habitat, alpine wetlands, with habitat specificity contributing to rarity in this region (Rabinowitz 1981). The most significant threat to these rare populations may be habitat alteration and loss, as a result of peat mining and the draining of wetlands for irrigation of surrounding ranchlands and diversion to municipal drinking water supplies. Although *C. viridula* has been assigned a state ranking of S1, indicating that it is critically imperiled in Colorado, it has received a global ranking of G5, indicating that it is demonstrably secure globally (Spackman et al. 1997).

Extant Colorado populations of *C. viridula* are geographically marginal, occurring at the edge of the species distribution in North America. Furthermore, North American populations, in general, are peripheral relative to West Europe, the putative center of diversity and origin for *C. viridula* (Crins and Ball 1989). Genetic theory predicts differentiation of marginal populations with respect to central populations, with reduced levels of genetic variation and greater population differentiation (Bruederle 1999). While marginal populations are expected to maintain a subset of the genetic variation observed in central populations as a result of reduced gene flow (Yeh and Layton 1979), both random genetic drift and selection may cause the fixation of alleles that are rare in central populations (Blows and Hoffman 1993).

However, other factors in addition to distribution may influence levels and apportionment of genetic diversity in species. Geographical range, successional status, population size, life form, breeding system, and seed dispersal mechanism have all been demonstrated to have significant effects on genetic diversity and structure (Brown 1979; Hamrick et al. 1979; Loveless and Hamrick 1984; Karron 1987; Hamrick and Godt 1989; Hamrick et al. 1991; Barrett and Kohn 1991). Furthermore, levels and apportionment of genetic variation could be the consequence not only of life-history characteristics, but also of historical and evolutionary events such as genetic bottlenecks resulting from founder effect, glaciation, migration, and speciation (Lewis and Crawford 1995).

The purpose of this research is to describe genetic diversity and structure in populations of *C. viridula* from Colorado relative to other North American and West European populations. Collectively, the aforementioned influential factors lead to three specific predictions regarding population genetic diversity and structure in *C. viridula*. First, life-history characteristics, such as self-compatibility, restricted habitat, short-lived perennial growth, herbaceous habit, ruderal strategy, and small population sizes, are expected to confer low levels of within-population genetic variation (Schmid 1984a, b; Crins and Ball 1988, 1989; Bruederle and Jensen 1991). Second, deviations from Hardy-Weinberg equilibrium and heterozygote deficiency are expected as a result of the caespitose habit, which has been correlated with high levels of inbreeding and genetic substructuring. Finally, pronounced differentiation among populations is expected as a result of reduced gene flow, isolation, inbreeding, and genetic drift. It is expected that Colorado populations will be genetically differentiated from other North American populations, and that North American populations, in general, will be genetically differentiated from West European populations.

MATERIALS AND METHODS

Fifteen populations of *C. viridula* were sampled during the summers of 1998 and 1999 from the Pacific Northwest, Rocky Mountain, and Great Lakes regions of the United States and Canada (Fig. 1, Table 1). Sites were typically peatlands or other wetlands, with *C. viridula* occupying early successional microsites along the shores of streams, springs, ponds, creeks, and swamps; or along roadsides, ditches, and ruts (Table 1). Population samples ranged in size from six to 50 individuals. Because *C. viridula* is caespitose, samples obtained from discrete, well-spaced clumps were assumed to represent different individuals. At each site, whole vegetative culms were harvested, placed in separate plastic bags with moist paper towels, and kept refrigerated until extraction of soluble enzymatic proteins. Extraction procedures followed those previously reported in Bruederle and Fairbrothers (1986). Voucher specimens for each population

FIG. 1. Map of North America showing the locations of 15 *Carex viridula* subsp. *viridula* var. *viridula* populations sampled for allozyme analysis. Detailed locations are provided for seven Colorado populations. Population numbers correspond to those in Table 1.

have been deposited at the University of Colorado at Denver Herbarium and the University of Colorado Herbarium (COLO).

Electrophoresis and staining followed Bruederle and Fairbrothers (1986) and Bruederle and Jensen (1991). Three gel-buffer systems and 15 enzyme stains were used to resolve 21 putative loci using 10.5% starch gels (Sigma-Aldrich, Inc.). Isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (6PGD), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), and shikimic acid dehydrogenase (SkDH) were stained on a discontinuous histidine-HCl system (Gottlieb 1981). Aspartate aminotransferase (AAT), acid phoshatase (ACP), and glyceradehyde-3-phosphate dehydrogenase (G3PDH) were stained on a tris-citrate system (Soltis et al. 1983). Alcohol dehydrogenase (ADH), diaphorase (DIA), malic enzyme (ME), menadione reductase (MNR), superoxide dismutase (SOD), and triose phosphate isomerase (TPI) were stained on a discontinuous lithium-borate system (Soltis et al. 1983). Staining followed Soltis et al. (1983) with minor modifications for IDH, MDH, PGI, PGM, SkDH, ACP, G3PDH, ME, and TPI; Gottlieb (1973) for PGD and ADH; and Cardy et al. (1981) for AAT.

Electrophoretic allozyme phenotypes were interpreted genetically on the basis of segregation patterns, know substructure and intracellular compartmentalization of enzymes, and previously observed electrophoretic patterns (e.g., Bruederle and Fairbrothers 1986). Data were collected as individual genotypes; these data have been deposited at the University of Colorado at Denver Herbarium and are available upon request (LPB). Standards rep-

resenting most of the common electrophoretic variants for the section were incorporated into each of the gels to facilitate allele identification.

Data were analyzed using BIOSYS-1 (Swofford and Selander 1981) to obtain common measures of genetic diversity including proportion of polymorphic loci (P), mean number of alleles per locus (A) and per polymorphic locus (A_p), observed heterozygosity (H_o), and expected heterozygosity (H_e). The distribution of genetic variation within and among populations was calculated using Nei's (1973) gene diversity statistics and GENESTAT-PC (Lewis and Whitkus 1989). In order to assess differences in genetic diversity, data from North American populations were compared with data previously reported for European populations of this species using a t-test (Table 1; Bruederle and Jensen 1991).

RESULTS

The fifteen enzymes assayed for *C. viridula* are encoded by 21 putative loci: *AAT-1, AAT-2, ACP-1, ADH, DIA-1, DIA-3, G3PDH, IDH-1, IDH-2, MDH-1, MDH-2, ME, MNR, 6PGD, PGI-2, PGM-1, PGM-2, SkDH, SOD, TPI-1,* and *TPI-2.* Four additional loci (*MDH-3, PGI-1, ACP-2,* and *ACP-3*) were not included in the analysis, because they did not exhibit consistent activity or clearly interpretable banding patterns.

North American *C. viridula* maintains no genetic diversity based upon this sample of 15 populations and 21 loci. None of the loci examined were polymorphic. At every locus assayed, each of the 529 individuals was homozygous for the same allele; no heterozygosity or allozyme variation was observed

TABLE 1.   LOCATIONS AND SITE INFORMATION FOR 15 NORTH AMERICAN *CAREX VIRIDULA* MICHX. SUBSP. *VIRIDULA* VAR. *VIRIDULA* POPULATIONS SAMPLED FOR ALLOZYME ANALYSIS, AS WELL AS THREE WEST EUROPEAN POPULATIONS (BRUEDERLE AND JENSEN 1991).

Pop. no.	Country, state, and province	Sample size	Location	Latitude	Longitude	Estimated population size	Habitat and microhabitat description
1	CO, USA	50	Park Co., Colorado, High Creek Fen, 13 km (8 m) S of Fairplay on U.S. Rte. 285	39°05′N	105°58′W	1000	scattered throughout well-developed peatland; colonizing alongside the banks of a few streams
2	CO, USA	50	Park Co., Colorado, Sweet Water Ranch, 18 km (11 m) S of Fairplay on U.S. Rte. 285	39°03′N	105°58′W	1200	scattered throughout well-developed peatland; colonizing alongside large, deep ditch dug through peatland
3	CO, USA	50	Park Co., Colorado, Warm Springs Ranch, 5 km (3 m) S of Fairplay on U.S. Rte. 285	39°09′N	106°03′W	100	growing on shore of spring and on moist areas adjacent to spring, alongside shore of pond
4	CO, USA	50	Jackson Co., Colorado, Lone Pine, 23 km (14 m) W of Walden on Co. Rd. 16	40°44′N	106°34′W	50	shore of pond, colonizing edge of one bank and on top of a few hummocks
5	CO, USA	50	Jackson Co., Colorado, Bear Creek, 24 km (15 m) W of Walden on Co. Rd. 16	40°45′N	106°35′W	50	shore of creek, colonizing along fallen log and within adjacent rut
6	CO, USA	50	Grand Co., Colorado, Haystack Mountain, 16 km (10 m) N of Silverthorne on St. Rte. 9	39°55′N	106°19′W	75	near outlet of small alkaline spring, some peat accumulation, growing on top of small hummocks
7	CO, USA	50	San Juan Co., Colorado, Andrew's Lake, 10 km (6 m) S of Silverton on U.S. Rte. 550	37°43′N	107°42′W	1000	scattered throughout well-developed peatland; colonizing shores of a few ponds
8	OH, USA	28	Ottawa Co., Ohio, Quarry Rd., 1 km (0.6 m) SW of Lakeside on St. Rte. 163	41°31′N	82°45′W	1000	scattered through moist areas in floor of old limestone quarry
9	MI, USA	27	Iosco Co., Michigan, 6 km (4 m) W of U.S. Rte. 23, N of Alabaster Rd.	44°12′N	83°37′W	500	adjacent to swamp, colonizing burrow pit
10	MI, USA	25	Mackinac Co., Michigan, 13 km (8 m) N of U.S. Rte. 2, W of Borgstrom Rd.	46°12′N	85°21′W	50	well-drained edge of sandy road
11	WI, USA	27	Waushara Co., Wisconsin, Hills Lake, 6 km (4 m) E of St. Rte. 22, S of Co. Rd. H	44°09′N	89°09′W	100	shore of lake; growing in rows of recent, successive colonizations

TABLE 1. CONTINUED.

Pop. no.	Country, state, and province	Sample size	Location	Latitude	Longitude	Estimated population size	Habitat and microhabitat description
12	WA, USA	28	King Co., Washington, Snoqualmie Bog, 21 km (13 m) E of St. Rte. 203, N of N. Fork Co. Rd.	47°40′N	121°37′W	1000	scattered throughout large bog/fen system underlain by peat soil
13	ONT, CAN	25	Norfolk Co., Ontario, Long Point on Lake Erie, 48 km (30 m) S of Hwy. 401	42°34′N	80°25′W	100	colonizing middle and edges of raised vehicular track
14	ONT, CAN	6	Peterborough Co., Ontario, Belmont Lake, 24 km (15 m) N of Hwy. 7	44°40′N	78°80′W	100	shore of lake
15	ONT, CAN	13	Nipissing Dist., Ontario, Radiant Lake, Algonquin Prov. Park, 16 km (10 m) N of Rte. 60	45°60′N	78°30′W	100	shore of lake
16	AUS	3	Trunnahütte, Austria, 3.8 km (2.4 m) SSW of Trin	47°30′N	11°70′E	na	growing in seepage at base of slope
17	SWE	26	Åsa, Sweden, 0.9 km (0.56 m) WSW	58°65′N	11°80′E	na	colonizing along hummocks and in depressions in saturated soils of meadow
18	SWE	28	Skanör, Sweden, 1 km (0.62 m) E	56°10′N	12°90′E	na	colonizing around rocks, hummocks, and in depressions of low, pastured meadow

(Table 2). As such, for all populations, the proportion of loci polymorphic (P), observed heterozygosity (H_o), and expected heterozygosity (H_e) were all zero. Similarly, the number of alleles per locus (A) was one, the minimum value for this statistic (Table 3).

While low, West European populations exhibited higher levels of genetic diversity than North American populations (Bruederle and Jensen 1991). On average, two of the 20 loci examined for West European populations (10.0%) were polymorphic (Table 2). Mean number of alleles per locus was 1.15, while mean number of alleles per polymorphic locus was 2.0. Observed heterozygosity was 0.014 and expected heterozygosity was 0.039 (Table 3). Genetic diversity in West European populations was significantly higher than that in North American populations when compared using a two sample t-test assuming unequal variances for proportion of polymorphic loci ($P < 0.10$), mean number of alleles per locus ($P < 0.05$), observed heterozygosity ($P < 0.05$), and expected heterozygosity ($P < 0.10$).

Levels of genetic diversity for the species across its sample range in North America and West Europe were extremely low. The mean proportion of polymorphic loci was 1.7%. Mean number of alleles per locus was 1.03, while mean number of alleles per polymorphic locus was 2.0. Observed heterozygosity was 0.002 and expected heterozygosity was 0.007 (Table 3).

Despite the differences in levels of genetic diversity, West European and North American populations are, in fact, very similar. Mean genetic identity obtained from pairwise comparisons of populations from North America and West Europe was 0.987. Mean genetic identity among North American populations was 1.000, and among European populations was 0.974, ranging from 0.960 to 1.000 for the latter. Of the small amount of diversity maintained by populations of *C. viridula*, the majority ($G_{st} = 0.650$) was due to differences among populations, both among West European and between North American and West European populations.

TABLE 2. ALLELE FREQUENCIES AT THREE POLYMORPHIC LOCI FOR 18 POPULATIONS OF *CAREX VIRIDULA* MICHX. SUBSP. *VIRIDULA* VAR. *VIRIDULA*. Population numbers correspond to those in Table 1. See text for allozyme nomenclature.

Locus	Allele	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
		North American Populations															European Populations		
PGI-2	b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
	c	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96
ADH	a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.07
	b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	0.93
SOD	a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.667	1.00	0.96
	b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.333	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04

DISCUSSION

As expected, North American populations of *C. viridula* do maintain extremely low levels of genetic diversity within populations. However, due to the low levels of genetic diversity within populations and subsequent lack of allozyme markers, no genetic differentiation was observed among populations in Colorado or North America. Nevertheless, North American populations were genetically differentiated from West European populations, with significantly more diversity maintained by West European populations. A number of factors could have contributed to the paucity of genetic diversity observed in populations of this species.

First, the plant allozyme literature reveals strong associations between genetic diversity and breeding system, with those species characterized by outcrossed breeding systems having significantly higher levels of genetic diversity apportioned among individuals within populations. On average, species characterized by selfing breeding systems maintain significantly lower levels of genetic diversity, including proportion of polymorphic loci, number of alleles per locus and per polymorphic locus, and observed heterozygosity (Brown 1979; Hamrick et al. 1979; Loveless and Hamrick 1984; Hamrick and Godt 1989; Hamrick et al. 1991).

Carex viridula has been shown to exhibit population genetic structure and seed set suggestive of selfing (Schmid 1984a; Bruederle and Jensen 1991). The extremely low levels of genetic variation found in North American populations of *C. viridula* in this study may be the result, in part, of such selfing. High levels of inbreeding attributable to selfing are expected to result in homozygosity and decreased genetic variability. Of the large number of species of vascular plants that have been examined similarly, at least 14 other taxa have been reported to maintain no detectable allozyme diversity (Table 4). Although an exact comparison between these taxa and *C. viridula* is not possible, it is noteworthy that almost all of these taxa also show substantial levels of selfing.

In graminoids, high levels of inbreeding have also been correlated with the caespitose growth form. Stebbins (1950) proposed a relationship between growth form and breeding system among grasses, suggesting that species with a rhizomatous growth form are predominantly outcrossing due to the intermingling of genets. In contrast, the caespitose habit results in a growth form in which the nearest neighbor of a flowering culm is another culm from the same plant (e.g., ramet), thus promoting inbreeding, and specifically, selfing. Genetic evidence substantiating this phenomenon in the graminoid genus *Carex* was first reported by Bruederle and Fairbrothers (1986) and Bruederle (1987). Additional evidence supporting the relationship between growth form and genetic variability in *Carex*

TABLE 3. SUMMARY OF GENETIC DIVERSITY FOR 18 POPULATIONS OF *CAREX VIRIDULA* MICHX. SUBSP. *VIRIDULA* VAR. *VIRIDULA*: SAMPLE SIZE (N), MEAN NUMBER OF ALLELES PER LOCUS (A) AND PER POLYMORPHIC LOCUS (A_p), PROPORTION OF POLYMORPHIC LOCI (P), OBSERVED HETEROZYGOSITY (H_o), AND EXPECTED HETEROZYGOSITY (H_e). Population numbers correspond to those in Table 1. A locus was considered polymorphic if the frequency of the most common allele did not exceed 0.95.

Pop. No.	N	A	A_p	P	H_o	H_e
1	50	1.0	—	0.0	0.000	0.000
2	50	1.0	—	0.0	0.000	0.000
3	50	1.0	—	0.0	0.000	0.000
4	50	1.0	—	0.0	0.000	0.000
5	50	1.0	—	0.0	0.000	0.000
6	50	1.0	—	0.0	0.000	0.000
7	50	1.0	—	0.0	0.000	0.000
8	28	1.0	—	0.0	0.000	0.000
9	27	1.0	—	0.0	0.000	0.000
10	25	1.0	—	0.0	0.000	0.000
11	27	1.0	—	0.0	0.000	0.000
12	28	1.0	—	0.0	0.000	0.000
13	25	1.0	—	0.0	0.000	0.000
14	6	1.0	—	0.0	0.000	0.000
15	13	1.0	—	0.0	0.000	0.000
Mean-N. America	529	1.0	—	0.0	0.000	0.000
16	3	1.15	2.0	15.0	0.017	0.070
17	26	1.05	2.0	5.0	0.006	0.006
18	28	1.25	2.0	10.0	0.018	0.042
Mean-W. Europe	57	1.15	2.0	10.0	0.014	0.039
Mean-Species	586	1.03	2.0	1.7	0.002	0.007

was subsequently provided by Ford et al. (1991, 1998).

A survey of the population genetic literature for the genus *Carex* revealed data for 29 taxa including six rhizomatous and 23 caespitose carices (Kuchel, unpubl.). On average, populations of rhizomatous species harbor high levels of genetic diversity, e.g., $A_p = 2.26 \pm 0.12$, $P = 44.5 \pm 4.08\%$, and $H_e = 0.171 \pm 0.038$, while caespitose species have significantly less, e.g., $A_p = 2.03 \pm 0.09$ ($P < 0.05$), $P = 13.4 \pm 12.0\%$ ($P < 0.001$), and $H_e = 0.042 \pm 0.04$ ($P < 0.001$). Furthermore, whereas populations of rhizomatous species are poorly differentiated ($G_{st} = 0.159 \pm 0.053$), caespitose species are well-differentiated with nearly half of all genetic diversity attributable to differences among populations ($G_{st} = 0.462 \pm 0.272$). Although exceptions exist (Ford et al. 1998), it would appear that rhizomatous species maintain more variation within and less differentiation among populations, presumably due to outcrossing. Conversely, caespitose species have less variation within and more differentiation among populations, presumably due to inbreeding. As such, the extremely low levels of genetic variation found in North American populations of *C. viridula* in this study may be the result, in part, of the caespitose growth form.

Second, narrowly distributed plant species tend to maintain lower levels of genetic variation than more widespread species (Karron 1987; Karron et al. 1988; Hamrick and Godt 1989). The lower levels of genetic variation observed in narrowly distributed species may be due to changes in allele frequencies due to chance (genetic drift and founder effect) or strong, directional selection toward genetic uniformity in a limited habitat type (Karron 1987). Almost all of the aforementioned genetically invariable taxa are narrowly distributed (Table 4).

Wolff and Jefferies (1987) hypothesized that the lack of diversity in one of these taxa, *Salicornia europaea* L., could be due to its restricted ecological distribution, despite the fact that it is geographically widespread. Ecologically, this species is confined to chronically disturbed, early successional open habitats in coastal and inland salt marshes where individuals and populations are subject to considerable turnover and population re-establishment. The narrow habitat requirements, founding events, small population sizes, and possible selection pressures experienced in such an environment could have contributed to the observed paucity of genetic diversity in *S. europaea*.

Even though *Carex viridula* is distributed throughout boreal North America, its ecological distribution also appears to be narrow. *Carex viridula* is a habitat specialist, occurring only in highly disjunct wetland habitats. Additionally, *C. viridula* is confined to early successional microsites, which tend to be small, ephemeral, highly variable, and subject to repeated local extinction and colonization. As in *Salicornia europaea*, it is possible that the extremely low levels of genetic variation found in populations of *Carex viridula* in this study may be, in part, the result of this narrow ecological distribution.

It is interesting to note that a number of species

TABLE 4. SUMMARY OF ALLOZYME LITERATURE FOR THOSE SPECIES HAVING NO DETECTABLE ALLOZYME VARIATION.

Species	Breeding system	Geographic range/ Ecological amplitude	Inferred historical mechanisms	Reference
Carex viridula	selfing	narrow distribution ecologically	Genetic drift: inbreeding and genetic bottleneck associated with founding events and/or climate changes during glaciation Rapid colonizer Disturbed habitats	
Bensoniella oregona (Abrams & Bacig) Morton	selfing	narrow distribution geographically	Genetic drift: inbreeding and genetic bottleneck associated with range restrictions during glaciation Clonal growth Small population sizes	Soltis et al. 1992
Chrysosplenium iowense Rydb.	selfing	narrow distribution geographically and ecologically	Genetic drift: inbreeding and genetic bottleneck associated with climate changes during glaciation Clonal growth Small population sizes	Schwartz 1985
Howellia aquatilis Gray	approaches obligate selfing	narrow distribution geographically and ecologically	Genetic drift: inbreeding and genetic bottleneck associated with range restrictions during glaciation Age of populations, not enough time to accumulate variability and heterozygosity	Lesica et al. 1988
Lespedeza leptostachya Engelm.	selfing	narrow distribution geographically	Genetic drift: inbreeding and genetic bottleneck associated with range restrictions during glaciation	Cole and Biesboer 1992
Oenothera hookeri Torr. and Gray	selfing	narrow distribution geographically	Genetic drift: inbreeding Age of populations, not enough time to accumulate variability and heterozygosity Rapid colonizer Permanent translocation heterozygosity	Levy and Levin 1975
Pedicularis furbishiae S. Wats	pollinator required for pollination, but possibly self-compatible	narrow distribution geographically and ecologically	Genetic drift: inbreeding and genetic bottleneck associated with range restrictions during glaciation and/or founding events Local population extinctions Disturbed habitats	Waller et al. 1987
Pinus resinosa Ait.	highly self-compatible	widespread geographically	Genetic drift: inbreeding and genetic bottleneck associated with range restrictions during glaciation Age of populations, not enough time to accumulate variability and heterozygosity	Fowler and Morris 1977; Allendorf et al. 1982; Simon et al. 1986; Mosseler et al. 1991

TABLE 4. CONTINUED.

Species	Breeding system	Geographic range/ Ecological amplitude	Inferred historical mechanisms	Reference
Salicornia euro-paea L. (s.l.)	selfing	narrow distribution ecologically	Genetic drift: inbreeding and genetic bottleneck associated with range restrictions during glaciation and founding events Rapid colonizer	Jefferies and Gottlieb 1982; Wolff and Jefferies 1987
Senecio mohav-ensis Gray	obligate selfing	narrow distribution geographically	Genetic drift: genetic bottleneck associated with founding events (recent colonization of North America) and/or climate changes during glaciation Rapid colonizer	Liston et al. 1989
Sullvantia ore-gana S. Wats.	selfing	narrow distribution geographically and ecologically	Genetic drift: inbreeding and genetic bottleneck associated with range restrictions during glaciation	Solits 1982
Taraxacum obli-quum (Fr.) Dahlst.	agamospermous	narrow distribution geographically and ecologically	Post-glacial range expansion through hybridization to form polyploid agamospermous populations Selection in more severe and less diverse environments	Van Oostrum et al. 1985
Thuja plicata Donn ex D. Don	self-compatible	narrow distribution geographically	No explanation given Genetic bottleneck associated with range restrictions unlikely; no evidence of physical barriers and associated species show abundant genetic variation	Copes 1981
Tragopogon pratensis Ownbey	selfing	widespread geographically	Genetic drift: inbreeding Rapid colonizer	Roose and Gottlieb 1976
Typha domin-gensis Pers.	selfing	widespread geographically and ecologically	Genetic drift: inbreeding Clonal growth Rapid colonizer Disturbed habitats	Mashburn et al. 1978; Sharitz et al. 1980

reported to maintain no detectable allozyme diversity are rapid colonizers of disturbed habitats (Table 4). *Carex viridula* has also been described as a rapid colonizer and ruderal species with rapid growth and development, small size, short life-span, early reproduction, large reproductive effort, and small population size (Schmid 1984a, b). In Switzerland, *C. viridula* often occupies newly disturbed sites, with many small and isolated populations. It is a pioneer in open, wet habitats, but is quickly excluded successionally (Schmid 1986). Not surprisingly, most populations sampled for this study appear to occupy early successional microsites, growing along pond shores, stream banks, roadsides, ditches, and ruts, comprising a part of larger, later successional communities (Table 1). Schmid (1984b) hypothesized that such ruderal species with early successional populations would have high ge-

netic variability between, but low genetic variability and high plasticity within populations, as a result of small population size, genetic drift, and directional selection. This hypothesis is supported by the ecology of *C. viridula* (Schmid 1984b), as well as the present study of genetic diversity.

Thus, low levels of genetic diversity found within populations of *C. viridula* may be attributed, in part, to effective breeding system and restricted ecological distribution. However, populations of this species in North America show substantially lower levels of genetic variability, even when compared to those means reported for selfing or narrowly distributed species—it should be reiterated that all putative loci examined were monomorphic. The most likely explanation for such low levels of polymorphism and heterozygosity is genetic drift. It is possible that a genetic bottleneck occurred at

some point in the history of these populations that eliminated all or most of the allozyme polymorphism.

One possibility is that a genetic bottleneck resulted from the founding of North American populations. During migration and dispersal, new populations may be formed by a small number of initial colonists. The genetic material of such populations is limited to those alleles introduced by these few founders and may not be representative of the species as a whole (Schwaegerle and Schaal 1979). Since European populations are the proposed progenitors of North American populations (Crins and Ball 1989), it would be expected that the allozymes present in North American populations would largely comprise a subset of those alleles present in European populations (Crawford 1983; Cole and Biesboer 1992). Indeed, North American populations are genetically differentiated from West European populations, with West European populations of *C. viridula* harboring higher levels of genetic diversity, and North American populations harboring a subset of that genetic diversity. These data suggest that a small number of individuals from the putatively ancestral European populations founded North American populations. Limited gene flow between populations would likely maintain the lower levels of genetic diversity observed in North American populations. Although populations of *Bromus tectorum* L. have only recently been introduced to North America from Eurasia, a number of similarities can be seen between this species and *C. viridula*. Both species exhibit low genetic variability within and high differentiation among populations possibly as a result of founding events and a selfing breeding system. Ecologically, both are characterized by routinely disturbed habitats and high phenotypic plasticity (Novak et al. 1991).

Another possibility is that a genetic bottleneck occurred at some point after the founding of North American populations. This bottleneck could have resulted in genetic uniformity in an original population or populations with a reduced geographic distribution, followed by spread of this species to the range now occupied (Lesica et al. 1988; Cole and Biesboer 1992). Climatic changes during the Pleistocene, particularly the Xerothermic period about 8500 to 3000 y B.P., have been suggested as a possible cause for genetic bottlenecks in a number of other North American species exhibiting extremely low levels of genetic diversity (Table 4), as well as in other species of *Carex* (Waterway 1990). Additionally, it has been suggested that these populations have not had enough time to accumulate variation and differentiate since these events (Levy and Levin 1975; Ledig and Conkle 1983; Lesica et al. 1988; Liston et al. 1989).

It has been suggested that allozyme variation detectable by electrophoresis may not provide a complete measure of genetic diversity in the genome (Mosseler et al. 1991; Mosseler et al. 1992). A more direct analysis of variation in DNA, e.g., RAPDs, may provide the genetic markers necessary to infer genetic diversity and structure in *C. viridula*. Data from the present study do indicate that *C. viridula* is genetically depauperate over a large portion of its range. However, additional analyses of populations lying at the extreme northwestern, northeastern, and eastern edges of the distribution in North America, as well as in putative glacial refugia, should be carried out to confirm this. Analyses of additional Eurasian populations would also contribute to a reconstruction of the biogeography of *C. viridula*.

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THE TAXONOMIC HISTORY, IDENTITY, AND DISTRIBUTION OF THE NEVADA ENDEMIC, *PLAGIOBOTHRYS GLOMERATUS* (BORAGINACEAE)

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Abstract

Plagiobothrys glomeratus A. Gray is a western Nevada endemic restricted to areas of altered andesite. It is morphologicaly close to *P. hispidus* A. Gray. *Plagiobothrys hispidus* is more widespread and shows much variation as to number and size of nutlets. Reports of *P. glomeratus* from California are based on misidentifications of *P. hispidus*. Illustrations of the nutlets and a distribution map of both species are included.

Current floristic studies in the Pine Nut Mountains of western Nevada uncovered a problem in defining *Plagiobothrys glomeratus* A. Gray. This study was undertaken to clarify the identity and distribution of *P. glomeratus*.

Gray (1885) described *Plagiobothrys glomeratus* from two collections by Katharine Curran (later Brandegee) taken between Virginia City and Carson City, Nevada. In the same article Gray described *P. hispidus* A. Gray based on a collection, again taken by Curran, from the streets of Truckee in nearby California. These two sites are approximately 27 air miles apart. Both taxa are members of section *Plagiobothrys* characterized by alternate leaves, lateral nutlet scars placed near or above the center of the nutlets, and not growing in seasonally saturated soils. They share the characteristic of having rather broad upper cauline leaves with *P. jonesii* A. Gray and *P. kingii* (S. Watson) A. Gray. Both *P. kingii* and *P. jonesii* have elongated nutlet scars along the ventral keel and an earlier spring flowering time in contrast with nutlet scars about as wide as long, placed at the end of the ventral keel, and a later spring to summer flowering time in *P. hispidus* and *P. glomeratus*. As such *P. hispidus* and *P. glomeratus* are more similar to each other than to any other species.

The first treatment of *P. glomeratus* is that of Greene (1887) who described the genus *Sonnea* to accomodate *P. glomeratus, hispidus, jonesii,* and *kingii*. He later described *Sonnea foliacea* from the geographic area between the type localities of *P. glomeratus* and *P. hispidus* (Greene 1888).

Johnston (1923) published a synopsis of *Plagiobothrys* placing *glomeratus* and *hispidus* in his *Sonnea* group and *kingii* and *jonesii* in his *Amsinckiopsis* group. He also reduced Greene's *Sonnea foliacea* to a variety of *P. hispidus* and stated: "It is possible that the plant is a hybrid between *P. hispidus* and *P. glomeratus*."

Tidestrom (1925) in his Flora of Utah and Nevada recognized the distinctiveness of *P. hispidus* and *P. glomeratus* but followed Greene in placing them in the genus *Sonnea*. He also maintained *S. foliacea* as a good species.

Cronquist (1984) recognized *P. glomeratus* as an acceptable species with the comment "Reno south nearly to Carson City, rarely collected." The only other published references for the distribution of *P. glomeratus* in Nevada are from the south side of Peavine Mountain where it is reported as occurring in an open pine stand (Billings 1992; Williams et al. 1992).

Plagiobothrys glomeratus is not included or mentioned in any flora covering California (Abrams 1951; Jepson 1925, 1943; Messick 1993; Munz 1968; Munz, and Keck 1959). Since none of the above references mention *P. glomeratus* or place it in synonymy I assume they did not have any evidence to believe it occurred in California.

DeDecker (1990) reported *P. glomeratus* as new to California. Her records are Sweetwater Mountains, above Star City, *DeDecker 5677* (RSA!) and Sierra Nevada, "The Bluffs," 0.6 miles NNE of Mammoth Rock, *Bagley 3001* (personal herbarium of Mark Bagley, Bishop, California!). A check with Roxanne Bittman of the California Natural Diversity Data Base, in Sacramento, CA, revealed no other known specimens from California. The DeDecker and Bagley records are the basis for including *P. glomeratus* in the California Native Plant Society inventory of rare and endangered vascular plants of California (Skinner and Pavlik 1994). I find both of these specimens to be *P. hispidus*. The misidentifications likely come from the lack of understanding of *P. hispidus* not from the true nature of *P. glomeratus*. Few California references provide the nutlet size for *P. hispidus*. Munz and Keck (1959) and Abrams (1951) list the size as 1 mm while Messick (1993) lists the size as 1–1.5 mm. Cronquist (1959, 1984) twice has dealt with *P. hispidus* and his descriptions are essentially the same. The one slight difference is nutlet length, 1–2 mm in 1959 and 1–2 (2.5) in 1984.

I have found that the nutlets of *Plagiobothrys hispidus* vary in the number that mature. At the north end of its range many plants have four ma-

turing nutlets while at the south end one or two is the norm. The number of maturing nutlets greatly influences their orientation, shape, and size. If four nutlets mature they are vertically oriented, less than 2 mm long, have a definite dorsal keel, and are unevenly tuberculate or rugose-tuberculate (see Fig. 1, illustration A). This is the nutlet type illustrated in Cronquist (1959, 1984) and represented by the type collection of *P. hispidus*. When one or two nutlets mature they are horizontally oriented, up to 2.4 mm long, flat-backed with a more obscure keel, the end farthest from the scar is greatly expanded, and the roughness is more evenly appressed and not as evident. It is this nutlet type that is represented by *DeDecker 5677* and *Bagley 3001*, the basis of the reports of *P. glomeratus* from California, and by the type of *Sonnea foliacea* (see Fig. 1, illustration C). On the other hand *P. glomeratus* is extremely uniform with larger, mottled, shiny nutlets, and is edaphically restricted (see Fig. 1, illustration D).

I can see how one could be misled in trying to identify the California specimens. The nutlet size does not fit the descriptions in Munz and Keck (1959) or Messick (1993). In checking Intermountain Flora (Cronquist 1984) the illustration of *P. hispidus* is that of the smaller four nutlet type. The broad fat-ended illustration of *P. glomeratus* then becomes the logical choice.

I agree with Cronquist (1984) in placing *Sonnea foliacea* in synonymy with *P. hispidus*. The extremes seem distinctive but all stages of intermediacy occur. For instance, many collections from the Truckee, CA area contain plants with nutlets of both the *hispidus* and *foliacea* type.

Gray (1885) in describing *P. glomeratus* describes its distributions as: "Western part of Nevada, between Carson and Virginia City, 1883 and 1884, Mrs. Layne-Curran." There are two sheets in the Gray Herbarium that fit Gray's protologue. One is labeled "Geiger Grade, Aug. 1883, *Curran s.n.*" and the other "between Carson and Virginia, [undated], *Curran s.n.*" Selection of the "Carson to Virginia" sheet as a lectotype was effectively done by Cronquist (1984).

The results of this study indicate that *Plagiobothrys glomeratus* is a western Nevada endemic restricted to areas of altered andesite between 4860 and 6650 ft in elevation. These altered andesite areas have shallow azonal soils nearly totally lacking in nutrients and with an acidic pH (3.7–4.0) (Billings 1992). Soils are so nutrient poor that they are not able to support the ubiquitous sagebrush, *Artemisia tridentata* Nutt., or other shrubs in any number (Billings 1950, 1992). This lack of competition from shrubs has allowed relic stands of Sierran conifers to persist in isolated pockets. The altered andesite areas are orangish light-brown in surface color and are dotted with dark green conifers. As such they are a conspicuous feature on the hills around Reno (Billings 1950, 1992). Although concentrated in the Reno area there are outliers of altered andesite as far northeast as the Pah Rah Range, east to Ramsey in the Virginia Range, and south to the Sweetwater and White Mountains of California and *P. glomeratus* may eventually be found at some of these sites (Billings 1992).

Plagiobothrys glomeratus is known from the Virginia Range in Storey and Washoe Counties, Carson Range of the Sierra Nevada, foothills north of Reno, and from nearby Peavine Mountain, all in Washoe County (see Fig. 2). Its distribution nearly matches that of the only other known altered andesite endemic, *Eriogonum robustum* E. L. Greene (type also collected by Curran in 1884). Both occur less than six miles from California and eventually may be found there. Searches in the Truckee River canyon west of Reno, and near Markleeville south-southwest of Gardnerville, have so far proved fruitless.

Plagiobothrys hispidus occurs from south-central Oregon south and east through the eastern Sierra Nevada of California and Nevada to the Mammoth area in Mono and adjacent Madera Counties (see Fig. 2). There are outliers on Steens Mountain, Harney County, Oregon, Skeedaddle Mountain, Lassen County, California, Granite Range, Washoe County, Nevada, Pine Nut Mountains, Douglas County, Nevada, and the Masonic Hills and Sweetwater Mountains in Mono County, California.

KEY TO *PLAGIOBOTHRYS GLOMERATUS* AND *HISPIDUS*

Nutlets smooth and shiny, mottled, 2.4–3.0 mm long, horizontally oriented, ... *P. glomeratus*
Nutlets unevenly tuberculate to pavemented with the roughness always readily discernable, up to 2.4 mm long, horizontally or vertically oriented. . . . . *P. hispidus*

Specimens of *Plagiobothrys glomeratus* examined, all from Nevada

STOREY CO., Virginia Range, Six Mile Canyon, 4.2 road miles E of highway 341, *Tiehm 12544* (BRY, CAS, NY, OSC, RENO, RSA, UC, UTC); Virginia Range, 1.1 road miles SE of N junction of highways 341 and 342 on highway 341, *Tiehm 12542* (ARIZ, BRY, CAS, GH, MONT, NY, OSC,

RENO, RM, RSA, UC, UNLV, UT, UTC, WS): WASHOE CO., Dandini Blvd. N of Reno, *Nachlinger 1375* (NY), *Tiehm & Kelley 12522* (CAS, NY, OSC, RENO, UC, UTC); west slopes of Peavine Mountain., *Nachlinger & Billings 1374* (NY); hill east of Black Panther Mine, 3 miles N of Reno, *Billings 1296* (RENO); Geiger Grade, Jul 1884, *Curran s.n.* (DS); Geiger Grade to Virginia City, *Eastwood 14809* (CAS); Geiger Grade, Aug 1883,
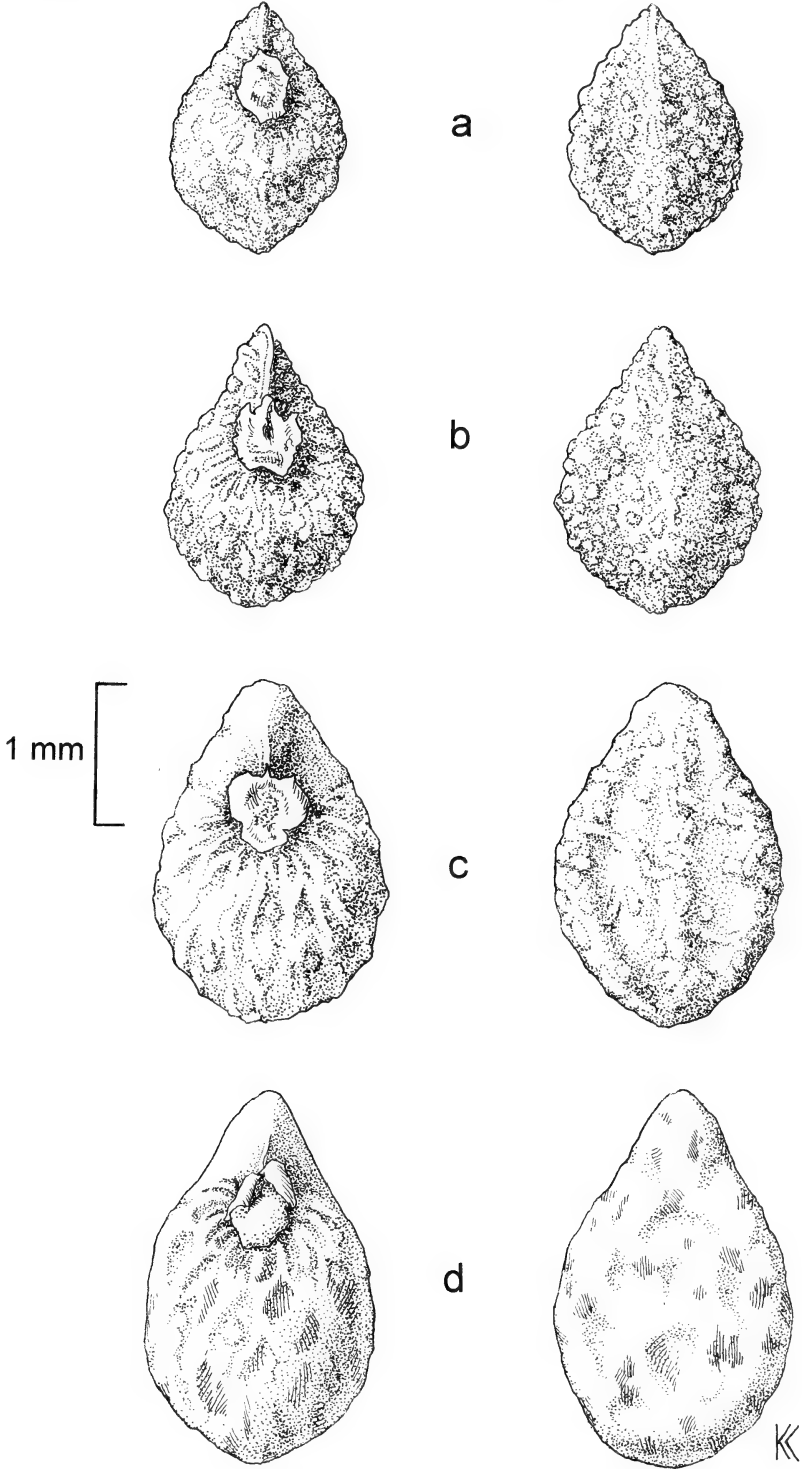
Fig. 1.   A–C are nutlets of *Plagiobothrys hispidus*, D is nutlets of *Plagiobothrys glomeratus*. A is drawn from *Steward 6798*, Deschutes Co., OR (NY); B from *Sonne s.n.*, Truckee, Nevada Co., CA (NY); C from *Tiehm 12244*, Pine Nut Mountains, Douglas Co., NV (RENO); and D from *Eastwood 14809*, Geiger Grade to Virginia City, Storey Co., NV (CAS).
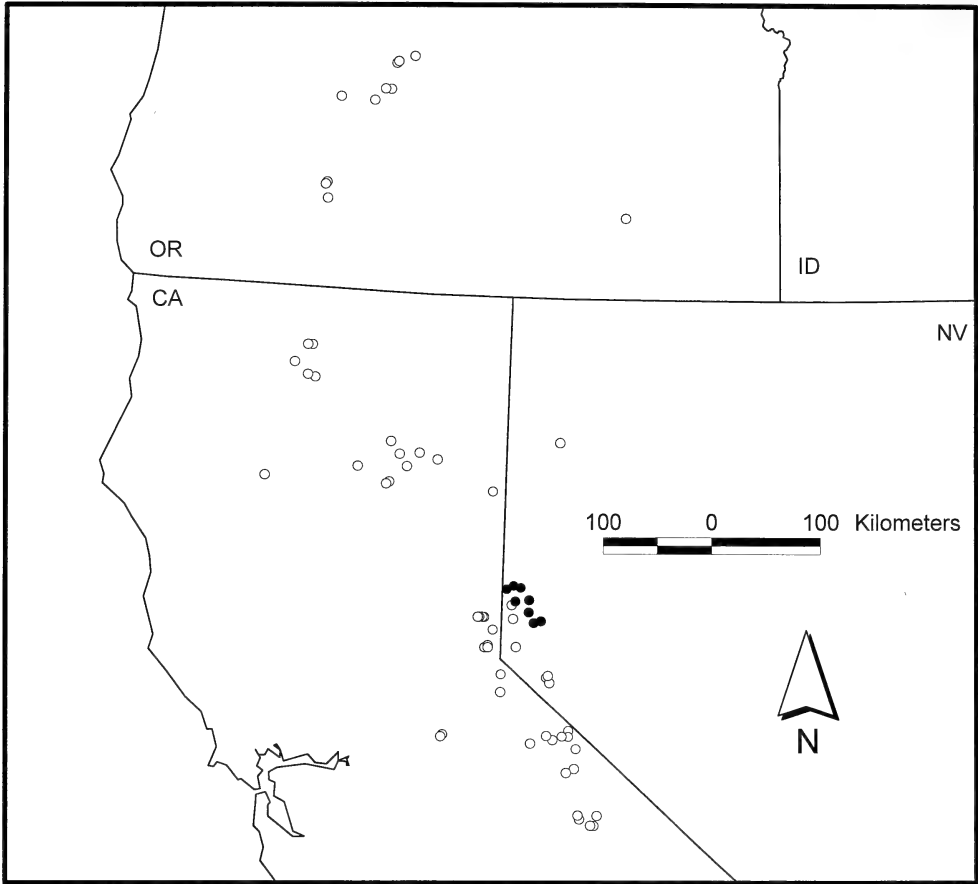
Fig. 2. Map showing parts of Oregon, Idaho, Nevada, and California. The distribution of *Plagiobothrys glomeratus* is designated by solid circles and the distribution of *P. hispidus* is designated by open circles.

Curran s.n. (GH); Virginia Range, Geiger Grade, 2.8 road miles E of highway 395 on highway 341, *Tiehm 12540* (ARIZ, ASU, B, BRY, CAS, COLO, CS, DAO, GH, ID, K, KSC, LE, MICH, MO, MONT, MONTU, NY, OKL, OS, OSC, RENO, RM, RSA, SI, TEX, UC, UNLV, UTC, WIS, WS, WTU); Virginia Range, foothills E of the S end of Hidden Valley County Park, *Tiehm 12547* (CAS, NY, OSC, RENO, RM, RSA, UC, UTC, WTU); Sierra Nevada, Carson Range, ridge on N side of N fork of Evans Creek, *Tiehm 12548* (BRY, CAS, MICH, MO, MONT, NY, OSC, RENO, RM, RSA, UC, UNLV, UTC); Sierra Nevada, Carson Range, ridge divide between Hunter and Alum Creeks, *Tiehm 12593* (CAS, NY, OSC, RENO, UC): COUNTY UNKNOWN, Nevada between Carson & Virginia, [undated], *Curran s.n.* (GH lectotype).

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GENETIC VARIATION IN *PINUS PONDEROSA, PURSHIA TRIDENTATA,* AND *FESTUCA IDAHOENSIS,* COMMUNITY-DOMINANT PLANTS OF CALIFORNIA'S YELLOW PINE FOREST

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Abstract

Genetic diversity of *Pinus ponderosa* Laws., *Purshia tridentata* (Pursh) DC., and *Festuca idahoensis* Elmer at Black's Mountain Experimental Forest in northwest California was evaluated using isozymes. This tree, shrub, and grass are all common, outcrossing, long-lived perennials that dominate their respective layers of the same plant community. Genetic analyses were provided for diploid *Pinus ponderosa* and *Purshia tridentata.* A phenotypic analysis of isozyme band patterns was provided for tetraploid *F. idahoensis* and, for comparison, previous reports of fescue isozyme variation were reanalyzed using this method. *Pinus ponderosa, Purshia tridentata,* and *Festuca idahoensis* were highly genetically variable, with 75% to 92% polymorphic loci. For all three species, more than 90% of the genetic variation occurred within, rather than among, populations.

This study compares genetic diversity in plant species of three life forms, while holding constant habitat, breeding system, and community dominance. The three plant species chosen for study are *Pinus ponderosa* Laws, *Purshia tridentata* (Pursh) DC, and *Festuca idahoensis* Elmer. They represent three life forms, tree, shrub, and grass, respectively. All three are common, widespread, outcrossing, long-lived perennials. All dominate their respective layers in the plant community at the study site. They do have life history differences; *F. idahoensis* is insect pollinated while the other two species are wind pollinated, and *F. idahoensis* is tetraploid while the others are diploid. The three species affect one another in a complex web of competitive and commensal relationships (e.g., Baron et al. 1966; Busse et al. 1996; Hall et al. 1995; vander Wall and vander Wall 1992).

The study site, Black's Mountain Experimental Forest, was established in 1934 in the Lassen National Forest, Lassen County, California. More than 60 y of experimentation and careful record keeping make the 4050-ha forest a uniquely valuable resource for investigating the effects of different timber management practices on eastside pine type forests. In 1993 the Black's Mountain Interdisciplinary Research Program was established to study the effects of forest management on various ecosystem components including vertebrates, insects, soil organisms, and vegetation. This study provides baseline data for a long-term study of effects of silvicultural treatments on genetic biodiversity. Genetic and species biodiversity are elements of a healthy ecosystem. Little is known about the effects of forest management on the genetics of forest plants, although some forestry practices can profoundly influence tree genetics (Adams et al. 1998).

Four plots similar in topography and vegetation were chosen for this study (Table 1). Genetic variation in the three selected species was sampled in 1994 and 1995. Subsequently, three silvicultural treatments (a timber cutting regime, fire, and grazing) were applied to the plots (Table 1). Genetic diversity will be resampled in five to twenty years, to detect any effects from the silvicultural practices initiated in 1995.

Methods

In 1993, plots were chosen for an intensive, multidisciplinary study of the effects of management practices on the entire ecosystem. Midpoints of the four plots were 2.2 to 4.0 km apart. These plots have been treated similarly in the past, and all were grazed lightly until 1996, when some were fenced to exclude cattle (Table 1). All four plots sampled in the genetics study consisted of dry forest dominated by *P. ponderosa,* and all plots were similar (Table 1). Half of each plot was subsequently burned. The presence of small, unburned, long-term control plots in some burned split plots is ignored in this analysis.

Sample collection. Permanent markers were established on a 100-m grid within each plot. In each plot, fifty grid points were randomly selected as

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TABLE 1.   CHARACTERISTICS AND MANAGEMENT PLANS OF THE FOUR BLACK'S MOUNTAIN PLOTS SAMPLED IN THIS STUDY. Pine trees are mostly Ponderosa Pine with some Jeffrey Pine; fir trees are White Fir, *Abies concolor* (Gordon and Glend.) Lindley. Perennial grass cover was predominantly Idaho Fescue cover. Structural vertical diversity is a management practice imposed by thinning two of the plots to reduce structural diversity. Half of each plot was subsequently burned; burned and unburned halves are labeled "B" and "N," respectively, in other tables. Information on plot vegetation from W. W. Oliver (unpublished data).

Plot	Elevation (meters)	Area (hectares)	Live trees/hectare		Idaho Fescue (frequency)	Perennial grasses (foliar cover)	Structural Vertical Diversity	Grazing
			Pine	Fir				
38	523–540	136	440	9	59%	4%	high	no
39	526–543	120	333	0	77%	6%	low	no
41	575–580	108	440	16	22%	2%	high	yes
43	570–576	109	364	170	40%	2%	low	yes

collection sites. All three species were collected at each grid point, if all three were present. If one or more was missing, a replacement sample was collected at a different, ranodmly selected grid point.

Pinus ponderosa: Cones were collected from the tree nearest each selected grid point (207 total individuals). Samples were collected in September 1994.

Purshia tridentata: At each selected grid point, two individuals were flagged and sampled (404 total individuals). The shrub closest to the grid point was the first sampled individual, and the second was the closest shrub on the opposite side of the gridpoint, on a line drawn from the first shrub through the grid point. A leafy shoot was cut from each individual, wrapped in wet paper towels, placed in a plastic bag, and stored on ice in the field. Samples were collected in June and July 1995.

Festuca idahoensis: Near each flagged *P. tridentata* shrub, a fescue individual was sampled (385 total individuals). (If fescue was sparse, the fescue might be as much as 30 meters away from the *P. tridentata*.) If no fescue grew within 30 meters of a sampling point, another point was randomly selected for fescue sampling. From each fescue, a small rooted plug with about 20 leaves was collected, wrapped in wet paper towels, placed in a plastic bag, and stored on ice in the field. Samples were collected in July 1995.

Sample preparation. Samples were prepared using NFGEL standard operating procedures (Anonymous 1995). For *P. ponderosa*, seeds were germinated and the megagametophytes were ground in a 0.2 M phosphate buffer, pH 7.5. The slurry was absorbed onto 3 mm wide wicks prepared from Whatman 3MM chromatography paper, and stored at −70°C. *Purshia tridentata* and *F. idahoensis* leaf tissue was ground in a Tris buffer pH 7.5 (Gottlieb 1981); liquid nitrogen was used to freeze *P. tridentata* tissue before grinding. One hundred fifty microliters of slurry per sample was transferred into each of two microtiter plate wells, and plates were

frozen at −70°C. For electrophoresis, the slurry was thawed and absorbed onto wicks.

Electrophoresis. Methods of electrophoresis are outlined in Anon. (1995), and follow the general methodology of Conkle et al. (1982) except that most enzyme stains are modified. The following enzymes were examined: aconitase (ACO), catalase (CAT), diaphorase (DIA), florescent esterase (FEST), fructose-1,6-diphosphate dehydrogenase (FDP), glutamate-oxaloacetate transaminase (GOT), glucose-6-phosphate dehydrogenase (G6PDH), glycerate-2-dehydrogenase (GLYDH), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucomutase (PGM), phosphogluconate dehydrogenase (6PGD), phosphoglucose isomerase (PGI), shikimic acid dehydrogenase (SKD), triosephosphate isomerase (TPI), and uridine diphosphoglucose pyrophosphorylase (UGPP). The enzymes examined, and the buffer systems used to resolve them, varied according to species (Table 2). All enzymes were resolved on 11% starch gels. Enzyme stain recipes for enzymes follow Anonymous (1995) except that GOT was stained using the recipe from Wendel and Weeden (1989). Two people independently scored each gel. When they disagreed, a third person resolved the conflict. For quality control, 10% of the individuals were run and scored twice.

Both *P. ponderosa* and the morphologically similar Jeffrey Pine *P. jeffreyi* Grev. and Balf (Jeffrey Pine) occur in the research plots (Oliver, MS). For a few of the pine samples, alleles of multiple enzymes differed from those seen before in *P. ponderosa* (NFGEL, unpublished data). Such samples were omitted from analysis on the assumption that they were *P. jeffreyi*.

Pinus ponderosa and *P. tridentata* are diploid. Most studied isozymes are known to show Mendelian inheritance in *P. ponderosa* (Linhart et al. 1989; O'Malley et al. 1979), but no such information is available for *P. tridentata*. Genetic interpretations were inferred directly from isozyme phe-

TABLE 2. ISOZYMES EXAMINED FOR *PINUS PONDEROSA*, *PURSHIA TRIDENTATA*, AND *FESTUCA IDAHOENSIS*. LB = a lithium borate electrode buffer (pH 8.3) used with a Tris citrate gel buffer (pH 8.3) (Conkle et al. 1982). SB = a sodium borate electrode buffer (pH 8.0) used with a Tris citrate gel buffer (pH 8.8) (Conkle et al. 1982). MC6 = a morpholine citrate electrode and gel buffer (pH 6.1) (Conkle et al. 1982). MC8 = a morpholine citrate electrode and gel buffer (pH 8.0) (Anon. 1985). na = number of alleles per locus. ne = effective number of alleles per locus (Kimura and Crow 1964). np = number of patterns per locus. For enzymes abbreviations, see text. Numbers in isozyme abbreviations refer to different regions on gels, interpreted as different loci.

Buffer: LB	na	ne	SB	na	ne	MC6	na	ne	MC8	na	ne
PINUS PONDEROSA											
ACO	4	2.8	CAT	1	1.0	FEST	7	1.5	DIA	4	2.9
ADH	2	1.9	GOT1	4	1.1	MDH1	3	1.0	FDP	1	1.0
LAP1	3	1.1	GOT2	5	1.1	MDH2	3	1.9	IDH1	3	1.7
LAP2	4	1.1	GOT3	6	1.3	MDH3	4	1.1	IDH2	5	1.2
ME	4	1.2	G6PDH	4	1.1				6PGD1	5	2.0
PGI1	2	1.0	UGPP1	3	1.9				6PGD2	4	1.1
PGI2	3	1.1	UGPP2	6	3.0						
PGM1	4	1.9									
PGM2	3	2.3									
PURSHIA TRIDENTATA	na	ne		na	ne					na	ne
FEST	1	1.0	CAT	2	1.0				DIA	2	1.0
LAP	3	2.6	GOT	4	2.6				FDP	3	1.0
PGI1	1	1.0	6PGD	4	1.1				IDH	1	1.0
PGI2	3	1.0	TPI1	2	1.0				MDH1	2	1.1
PGM	3	2.0	TPI2	1	1.0				MDH2	3	1.0
			UGPP	3	1.9						
FESTUCA IDAHOENSIS	np			np						np	
ME	1		CAT	1					DIA	6	
PGI	17		GLYDH	3					SKD	4	
PGM	3		GOT1	3							
			GOT2	4							
			6PGD	2							
			TPI	4							
			UGPP	16							

Row labels at left: "16 enzymes / 26 loci" (Pinus ponderosa), "13 enzymes / 16 loci" (Purshia tridentata), "11 enzymes / treated as 12 loci" (Festuca idahoensis).

notypes, based on knowledge of the generally conserved enzyme substructure, compartmentalization, and isozyme number in higher plants (Gottlieb 1981, 1982; Weeden and Wendel 1990). Genotypes of *P. ponderosa* were inferred from the segregation patterns of 10 megagametophytes per tree.

Festuca idahoensis has a chromosome number 2n = 28 and is thought to be autotetraploid (Darlington and Wylie 1955). Because of the complicated banding patterns observed, and because of lack of crossing studies to determine the inheritance of bands in this species, we were unable to identify specific alleles and loci for some enzymes, including highly variable MDH, PGI and UGPP. Therefore, a phenotypic instead of genotypic analysis was performed.

Data analysis. In order to allow future comparison with genetic diversity after all silvicultural techniques (logging, grazing, and burning) are implemented, the data were analyzed in terms of eight plots, which represent the half plots subsequently burned (Table 3).

For *P. ponderosa* and *P. tridentata,* results were analyzed using Popgene version 1.21 (Yeh et al. 1997). A locus was considered polymorphic if an alternate allele occurred at least once. Statistics calculated included unbiased genetic distances (Nei 1978), expected heterozygosity (Nei 1973), inferred gene flow (Nm = $0.25(1/F_{st})/F_{st}$; Slatkin and Barton 1989), and F statistics (F = $(H_e - H_o)/H_e$; Hartl and Clark 1989). The gene diversity statistics H_{es} (expected heterozygosity at the species level) and H_{ep} (expected heteozygosity at the population level) were calculated (Hamrick and Godt 1990).

For *F. idahoensis,* phenotypic diversity measures were calculated from both band presence/absence and multi-band patterns. For presence/absence data, phenotypic diversity was measured by a polymorphic index (PI), based on the frequency of occurrence of each band. PI = the sum of f(1−f), where f = the frequency of a band in a population (Chung et al. 1991). For multi-band patterns, phenotypic diversity measures include: (1) the number of bands found in each plot, (2) percent of stains that yield more than one band pattern, (3) the average number of band patterns per stain in each plot, and (4) Shannon-Weaver Diversity Index values (Shannon and Weaver 1949). The Shannon-Weaver Diversity Index uses the frequency of each band pattern in each plot. The larger the Shannon-Weaver Index,

TABLE 3.   SUMMARY OF GENETIC DIVERSITY MEASURES IN *PINUS PONDEROSA* AND *PURSHIA TRIDENTATA* BY SPECIES AND BY PLOT. All = overall statistics for the study. Mean = average over the 8 plots. SD = standard deviation. N = mean number of individuals sampled per locus, per population. %P = percent of all loci that are polymorphic. A = average number of alleles per locus. A_p = the average number of alleles per polymorphic locus. H_o = observed frequency of heterozygotes. H_e = frequency of heterozygotes expected under Hardy-Weinberg equilibrium conditions. F = the fixation index, = $(H_e-H_o)/H_e$ (* = statistically significant difference ($p < 0.05$)). S-W = Shannon-Weaver diversity index. B and N following plot numbers indicated the half plots that were subsequently burned or not burned.

	N	%P	A	A_p	H_o	H_e	F	S-W
Pinus ponderosa (26 loci)								
All	207	92%	3.73	3.96	0.264	0.272	0.030	0.510
Mean	26	85%	2.79	3.09	0.265	0.271	0.021	0.483
SD	2.4	4.0	0.11	0.10	0.021	0.010	0.082	0.019
38B	24	88%	2.73	2.96	0.263	0.269	0.023	0.477
38N	26	81%	2.73	3.14	0.251	0.264	0.046	0.470
39B	27	92%	3.04	3.21	0.283	0.287	0.012	0.517
39N	29	85%	2.81	3.14	0.240	0.277	0.133	0.495
41B	26	85%	2.73	3.04	0.280	0.280	0.002	0.495
41N	23	81%	2.77	3.19	0.257	0.255	−0.010	0.455
43B	23	88%	2.73	2.96	0.301	0.264	−0.140	0.467
43N	29	81%	2.77	3.09	0.244	0.272	0.104	0.489
Purshia tridentata (16 loci)								
All	404	75%	2.38	2.83	0.138	0.157	0.117*	0.263
Mean	50	55%	1.81	2.47	1.138	0.156	0.113	0.254
SD	8.0	9.6	0.12	0.26	0.006	0.005	0.049	0.011
38B	50	50%	1.69	2.38	0.135	0.148	0.087	0.235
38N	50	56%	1.69	2.22	0.134	0.152	0.120*	0.247
39B	62	38%	1.75	3.00	0.140	0.156	0.101	0.254
39N	38	50%	1.75	2.50	0.138	0.152	0.091	0.246
41B	52	69%	1.94	2.36	0.130	0.155	0.165	0.260
41N	50	62%	2.00	2.60	0.147	0.157	0.059	0.262
43B	42	52%	1.75	2.20	0.132	0.166	0.204*	0.269
43N	60	62%	1.94	2.50	0.147	0.159	0.076	0.261

the more diverse the plot. The distribution of the total variation within and among plots was determined by partitioning the total Shannon-Weaver Diversity Index. The phenotypic relationships among plots were determined by calculating Hedrick's phenotypic identities (Hedrick 1971) for multi-band pattern data, and by cluster and principle coordinate analyses of Jaccard's Similarity Index for band presence/absence data (Chung et al. 1991; Rolf 1987).

The hypothesis that all the plots had equal genetic diversity by species was tested by ANOVA using Excel (Microsoft 1997). In one analysis, plots were treated as blocks and the burned and unburned half plots as samples. In a second analysis, burned and unburned half plots were treated as blocks and the plots were treated as samples.

RESULTS

Pinus ponderosa, P. tridentata, and *F. idahoensis* were all genetically variable (Tables 3 and 4). Both percent polymorphic loci/enzyme and the Shannon-Weaver diversity index indicate that *P. tridentata* is the least variable of the three species.

In the two diploid species for which they could be calculated, observed heterozygosity nearly equaled that expected under Hardy-Weinberg conditions. Therefore, the fixation index (F) within each plot, calculated for *P. ponderosa* and *P. tridenta,* was low (F < 0.113) (Table 3). Although heterozygosity could not be calculated for *F. idahoensis,* we observed the unequal band staining and complex band patterns characteristic of heterozygous tetraploids (Soltis and Riesberg 1986).

F_{st} values indicated that over 98% of the isozyme variation in *P. ponderosa* and *P. tridentata* was within, rather than between populations, and inferred gene flow was high (Table 5). G_s, a measure of interpopulation diversity analogous to F_{st} but calculated from the Shannon-Weaver diversity index, was somewhat higher than the corresponding values of F_{st}, but indicated that in all three species more than 92% of the variation was within, rather than between, populations (Table 5).

Genetic similarities among plots were correspondingly high. Unbiased genetic identities (Nei 1978) between plots were greater than 0.99 for *P. ponderosa* and *P. tridentata.* Hedrick's distances (Hedrick 1971), calculated using band patterns, revealed a similarily greater than 0.98 for *F. idahoensis.* For *F. idahoensis,* band presence/absence data did not reveal differences between plots. No bands were unique to any plot. Two clusters appeared in a graph based on Jaccard's similarity index (not shown), but all eight plots were represented in both clusters.

TABLE 4. GENETIC VARIATION IN *FESTUCA IDAHOENSIS* AT BLACK'S MOUNTAIN, FOR 12 ENZYMES. All = overall statistics for the study. Mean = average over the 8 plots. SD = standard deviation. N = mean sample size/stain. #Bands = total number of bands (in all stains), in the population. %P* = percent of all presumed loci (regions on the gel that each probably represent a locus or set of homoeologos loci) that have more than one band pattern. A* = mean number of band patterns/stain. PI = polymorphic index based on band presence/absence data (see text). S-W = Shannon-Weaver diversity index is based on band patterns. B and N following plot numbers indicated the half plots that were subsequently burned or not burned.

	N	#Bands	%P*	A*	PI	S-W
All	385	53	83%	5.17	3.804	0.563
Mean	48.1	45.1	66%	3.41	3.666	0.521
SD	8.6	2.5	8.3%	0.24	0.211	0.015
38B	61	46	75%	3.83	3.400	0.535
38N	47	45	67%	3.33	3.639	0.498
39B	59	45	67%	3.58	3.851	0.543
39N	36	42	58%	3.08	3.840	0.511
41B	49	43	50%	3.17	3.536	0.527
41N	47	49	75%	3.58	3.530	0.525
43B	39	48	67%	3.33	4.013	0.516
43N	47	43	67%	3.42	3.520	0.510

With one exception, measures of genetic variability in plots 38, 39, 41, and 43 did not differ significantly for any of the three species. The only exception was the Shannon-Weaver diversity index for *P. tridentata*. Its Shannon-Weaver diversity index values differed significantly among plots (Table 6), and values for plot 43 are higher than those of plot 38. Before fire treatments were applied, measures of genetic variability were the same in all the half plots, except that the percent polymorphic loci and observed heterozygosity for *P. ponderosa* were consistently higher on the plots that would later be burned (Table 6).

The mean heterozygosity for the species (H_{es}) and the sampled populations (H_{ep}) (Hamrick and Godt 1990) were 0.271 and 0.266, respectively, for *P. ponderosa,* and 0.156 and 0.120 for *P. tridentata*.

DISCUSSION

Pinus ponderosa. Genetic variability found in this study is higher than previously reported in comparable studies of this species (that is, in studies that involved at least twelve loci and including both polymorphic and monomorphic loci) (Allen-

TABLE 5. INTER-POPULATION DIVERSITY STATISTICS IN *PINUS PONDEROSA, PURSHIA TRIDENTATA* AND *FESTUCA IDAHOENSIS* AT BLACK'S MOUNTAIN. G_s = a measure of inter-populational genetic differentiation derived from the Shannon-Weaver diversity index and analogous to F_{st}. F_{st} = Wright's fixation index (Weir 1990). S-W = mean Shannon-Weaver diversity index. Nm = inferred gene flow, = $0.25(1-F_{st})/F_{st}$.

Species	G_s	F_{st}	Nm
Pinus ponderosa	0.0406	0.0188	13.0301
Purshia tridentata	0.0708	0.0148	16.6675
Festuca idahoensis	0.0637		

dorf et al. 1982; Niebling and Conkle 1989; O'Malley et al. 1979; Woods et al. 1983; Yow et al. 1992). Expected heterozygosity (H_{es}) in this study equals 0.272 while the average H_{es} of the other studies equals 0.171. However, this level of genetic variability is consistent with previous NFGEL research on *P. ponderosa* (in previous NFGEL studies the average H_{es} = 0.231; NFGEL, unpubl.). The higher genetic variability reported by NFGEL for this species probably results from quality control measures and highly standardized procedures that allow repeatable detection of small differences in enzyme migration distances. Including rare alleles (those with frequencies lower than 0.05) in analyses may also contribute to the high genetic variability reported. Both NFGEL studies and previously published work indicate that *P. ponderosa* subsp. *ponderosa* is more genetically variable than *P. ponderosa* subsp. *scopulorum* (average from NFGEL studies: H_{es} (subsp. *ponderosa*) = 0.247, H_{es} (subsp. *scopulorum*) = 0.235; average from other studies: H_{es} (subsp. *ponderosa*) = 0.161, H_{es} (subsp. *scopulorum*) = 0.151).

Genetic variation in *P. ponderosa* was distributed within, rather than among, the plots. More than 90% of the isozyme variation often occurs within, rather than among, *P. ponderosa* populations (Hamrick et al. 1989, Linhart et al. 1981). Because *P. ponderosa* pollen can travel long distances (Latta et al. 1998), and calculated gene flow among plots in this study is high (Table 5), the short distances (2 to 4 km) between plots may limit genetic differentiation. However, genetic differentiation has been detected previously over small distances in *P. ponderosa* (Beckman and Mitton 1984; Mitton et al. 1977; Mitton et al. 1980). In general, the genetic similarily among plots provides a uniform background against which the genetic effects, if any, of timber management practices will be detectable. However, the higher initial percent polymorphic

TABLE 6. ANALYSIS OF VARIANCE OF MEASURES OF GENETIC VARIABILITY IN *PINUS PONDEROSA*, *PURSHIA TRIDENTATA* AND *FESTUCA IDAHOENSIS*. The fixation index $F = (H_e - H_o)/H_e$. The variance ratio $F = s_1^2/s_2^2$, where s^2 = the variance of the sample. * = statistically significant difference ($p < 0.05$).

Measure of genetic variance	Half plots (half later burned)		Plots 38, 39, 41 and 43	
	F (variance ratio)	probability	F (variance ratio)	probability
Pinus ponderosa				
N = number of individuals/plot	1.0576	0.3434	0.7233	0.5886
P = % polymorphic loci	12.755	0.0118*	0.5460	0.6767
A = alleles/locus	0.2242	0.6526	2.3785	0.2107
A_p = alleles/polymorphic locus	2.4440	0.1690	0.9505	0.4964
H_o = observed heterozygosity	14.627	0.0087*	0.1305	0.9370
H_e = expected heterozygosity	1.2605	0.3045	1.0604	0.4588
F = fixation index	3.5968	0.1067	0.3551	0.7893
SW = Shannon Weaver diversity index	0.6778	0.4418	1.4773	0.3478
Purshia tridentata				
N = number of individuals/plot	0.1076	0.7540	0.0059	0.9993
P = % polymorphic loci	0.5627	0.4815	3.8774	0.1117
A = alleles/locus	0.4615	0.5223	6.0143	0.0579
A_p = alleles/polymorphic locus	0.0238	0.8824	1.5350	0.3355
H_o = observed heterozygosity	3.2858	0.1198	0.1758	0.9076
H_e = expected heterozygosity	0.1197	0.7412	4.9700	0.0777
F = fixation index	2.9523	0.1366	0.2069	0.8868
SW = Shannon Weaver diversity index	0.0031	0.9574	6.6854	0.0489*
Festuca idahoensis				
N = number of individuals/plot	1.8075	0.2274	0.4115	0.7542
Number of bands/enzyme	0.1617	0.7015	0.2770	0.8401
%P* = % polymorphic enzyme	0.1005	0.7619	0.3481	0.7938
A* = number of patterns/enzyme	0.4906	0.5099	0.2970	0.8269
PI = polymorphic index	0.1811	0.6853	1.4484	0.3542
SW = Shannon Weaver diversity index	5.6936	0.0543	0.3223	0.8104

loci and observed heterozygosity in burned than in unburned half-plots (Table 6) would have been considered a treatment effect if this baseline study had not been done.

Purshia tridentata. Bitterbrush has been the subject of intense scrutiny, focused on interspecific relationships and management practices (e.g., Basile 1967) rather than genetic diversity. Secondary compounds have interferred with isozyme resolution in previous studies (S. Brunsfeld, pers. comm.). Genetic variation was less evenly distributed among plots in *P. tridentata* than in the other two species in this study (Table 3), possibly because *P. tridentata* is pollinated by insects, rather than wind. Although plots were homogeneous for most measures, there were significant differences in the fixation index (Table 3) and Shannon-Weaver diversity index (Table 6).

Festuca idahoensis. Because polyploidy complicates gel interpretation, isozymes have been underutilized for describing genetic variation in the fine-leaved fescues, *Festuca* subgenus *Festuca*, to which *F. idahoensis* belongs, and summary statistics are rarely reported. One should keep certain trends in mind when comparing a phenotypic analysis, like that performed for fescues, with genotypic analyses of isozymes. The proportion of polymorphic enzymes (%PE in Tables 7, 8) is higher than the percent polymorphic loci (%P*) because stains may

reveal both polymorphic and monomorphic loci for the same enzyme. %PE is reported because the statistic is unambiguous. Percent polymorphic putative loci (%P*) is theoretically equal to %P of a genetic analysis, although for polyploid plants different researchers may parse band patterns into loci in different ways. The number of patterns reported per putative locus (A*) should be somewhat greater than the number of alleles per locus, because any two alleles can produce three patterns. For example, AA homozygotes, BB homozygotes, and AB heterozygotes are counted as three different patterns. The polymorphic index (PI) is a rough measure of heterozygosity, valid only for comparing populations within a study. Measures of similarity and diversity based on patterns (Hedrick's distance and the Shannon-Weaver diversity index, respectively) may overestimate differences, because AA homozygotes, BB homozygotes, and AB heterozygotes are considered three equally different patterns. On the other hand, measures of similarity and diversity based on bands (Jaccard's Similarity Index and the polymorphic index, respectively) produce uneven results among monomeric enzymes (which have two bands when heterozygous), dimers (which have three), and tetramers (which have five) (Gottlieb 1977). The Gs statistic derived from partitioning the Shannon-Weaver diversity index, like hierarchical F-statistics (Wright 1978), indicates whether a greater proportion of variation resides within

TABLE 7. OVERALL ISOZYME DIVERSITY STATISTICS FOR TAXA *FESTUCA* SUBGENUS *FESTUCA*, FROM STUDIES THAT WERE NOT LIMITED TO POLYMORPHIC ALLELES. Overall statistics are total values for the entire study. Chr. = Chromosome number (2X = 14, etc.). † = chromosome numbers from Markgraf-Dannenberg (1980); other chromosome numbers were provided in the source article. Pops. = number of populations. N = mean sample size per population. Enz = number of enzymes stained. Loci = number of regions on the gel that each probably represent a locus or set of homoelogous loci. Summary statistics calculated by authors: %PE = percent of polymorphic enzymes. %P = percent of polymorphic putative loci. AE = number of patterns per enzyme. A* = number of patterns per putative locus.

Taxon	Chr.	Pops.	N	Enz.	Loci	%PE	%P*	AE	A*	Source
(*F. ovina* complex)										
F. auriculata	2X	4	20	10	15	90%	67%			1
F. baffensis	4X	3	26	10	15	90%	67%			1
F. brachyphylla	6X	5	23	10	15	80%	67%			1
F. brevissima	2X	2	23	10	15	20%	13%			1
F. idahoensis	4X	8	48	11	12	82%	83%		5.17	5
F. idahoensis	4X	8	41	11	18	91%	67%		2.67	4
F. minutilfora	2X	1	3	9	14	67%	21%			1
F. roemeri v. *klamathensis*	4X	4	31	11	18	91%	67%		2.78	4
F. roemeri v. *romeri*	4X	8	27	11	18	91%	72%		4.00	4
F. valesiaca	2X	3	31	8	20	75%	50%	2.75	1.65	2
(*F. rubra* complex)										
F. amythestina	2X†	2	58	8	20	62%	35%	2.25	1.40	2
F. asperifolia		1	40	8	20	75%	45%	2.25	1.65	2
F. diffusa	6X, 8X†	1	40	8	20	50%	20%	1.65	1.35	2
F. heterophylla	4X†	8	37	8	20	65%	40%	2.25	1.60	2
F. nigrescens	4X, 6X†	6	36	8	20	50%	35%	2.50	1.65	2
F. nigrescens	6X	3	27	11	18	82%	67%		2.33	4
F. peristerea		1	40	8	20	75%	30%	1.75	1.35	2
F. picturata		3	34	8	20	75%	35%	2.12	1.50	2
F. rubra	2X-10X†	8	20	8	20	75%	45%	2.88	1.75	2
F. rubra	6X	6	38	10		100%				3

Sources:
1 = Aiken et al. 1993
2 = Angelov and Edreva 1987 (omitting anodal esterase), Angelov et al. 1988, Angelov 1992, 1993
3 = Livesey and Norrington-Davies 1991
4 = Wilson 1999
5 = this study

or among populations. Although a phenotypic analysis is imprecise compared to genetic analyses of isozyme data, it does quantify isozyme variation and therefore allows comparisons among those polyploid taxa for which genetic interpretations are not possible.

Available studies indicate that these fescues are highly polymorphic (Tables 7, 8), with the excep-

TABLE 8. MEAN ISOZYME DIVERSITY STATISTICS PER POPULATION FOR *FESTUCA* SUBGENUS *FESTUCA*, FROM STUDIES THAT WERE NOT LIMITED TO POLYMORPHIC ALLELES. Chr. = Chromosomes (2X = 14, etc.). Chromosome numbers were provided in the source article. Pops. = number of populations. N = mean sample size per population. Enz = number of enzymes stained. Loci = number of regions on the gel that each probably represent a locus or set of homoeologos loci. Summary statistics calculated by authors: %PE = percent of polymorphic enzymes. %P* = percent of polymorphic putative loci. A* = number of patterns per putative locus. S-W = Shannon-Weaver diversity index.

Taxon	Chr.	Pops.	N	Enz.	Loci	%PE	%P*	AE	A*	Source
(*F. ovina* complex)										
F. auriculata	2X	4	20	10	15	60%	43%			1
F. brachyphylla	6X	5	23	10	15	67%	40%			1
F. brevissima	2X	2	23	10	15	68%	7%			1
F. idahoensis	4X	8	48	11	12	68%	66%	3.41		3
F. idahoensis	4X	2	56	11	18	68%	50%	2.03	0.2032	2
F. minutilfora	2X	1	3	9	14	67%	21%			1
F. roemeri v. *klamathensis*	4X	4	31	11	18	80%	53%	1.89	0.2376	2
F. roemeri v. *romeri*	4X	6	33	11	18	67%	50%	1.94	0.2710	2

1 = Aiken et al. 1993
2 = Wilson 1999
3 = this study

tion of the uncommon *F. brevissima* Jurtzev. Variability in Black's Mountain *F. idahoensis* was high but consistent with previously reported fescue genetic variation. Our reported number of band patterns per putative locus was particularly high but not anomalous. For example, we detected 17 PGI band patterns (Shannon-Weaver diversity index = 1.91), and the same number were found for PGI in a survey of 6 European Red Fescue (*F. rubra* L.) populations (S-W = 1.75) (Livesey and Norrington-Davies 1991). That study reported an average of 10 band patterns per enzyme in the three highly variable enzymes investigated.

Genetic distances and identities among fescue populations are rarely reported. Genetic identities between populations of diploid arctic fescues are 0.934 (*F. brevissima*) and an average of 0.857 (*F. auriculata* Drobov aggregate) (Aiken et al. 1993). In both intra- and interspecific comparisons, Hedrick's identities exceed 0.95 between populations in the tetraploid *F. idahoensis* and Roemer's Fescue (*F. roemeri* (Pavlick) E. B. Alexeev) species pair in northern California (Wilson 1999). The high (greater than 0.98) Hedrick's identities among Black's Mountain fescue populations are therefore expected.

Because Black's Mountain populations of *F. idahoensis* were similar, any effects of burning, grazing, and logging regimes on genetic variability will be detectable. Such fine-scale adaptation to local habitat variables has been seen in grasses, particularly in self-pollinating species (Bradshaw 1959; Clary 1975; Clegg and Allard 1972; Hamrick and Allard 1972; Kahler et al. 1980; Lönn 1993; Nevo et al. 1983). However, coarse adaptation has also been observed in both self- and cross-pollinated introduced grasses (Rice and Mack 1991; Rapson and Wilson 1988).

Summary. The gymnosperm tree *P. ponderosa,* the dicot shrub *P. tridentata,* and the monocot grass *F. idahoensis* are not phylogenetically close. However, they have strikingly similar patterns of electrophoretically detected genetic variation. All are genetically variable, with well over 90% of the variation within, rather than among, populations in the area studied. All three are common, widespread, long-lived, perennial, outcrossing species that dominate late successional stages in their plant community. Plants with this series of characteristics tend to be more genetically variable than average, and to have their genetic variation within, rather than among, populations (Hamrick and Godt 1990). The high level of genetic variability detected in the three plants is consistent with observed trends in genetic variability (Hamrick and Godt 1990).

The markedly lower genetic variation in *P. tridentata* as compared to the other two species is consistent with the tendency for insect pollinated plants and dicots to have much less isozyme vari-ation than wind pollinated plants and gymnosperms or monocots (Hamrick and Godt 1990).

The value of the genetic diversity statistics H_{es} and H_{ep} for *P. ponderosa* are more than one standard deviation higher than comparable mean statistics reported (Hamrick and Godt 1990; Hamrick et al. 1992). Those for *P. tridentata* vary from that far above to somewhat below average, depending upon the comparison; they are low for woody angiosperms (Hamrick et al. 1992), but most woody angiosperms studied are wind-pollinated trees, and *P. tridentata* is an insect-pollinated shrub. For all three species, the percentage of genetic variability among populations is lower than the mean reported in comparable plants (Hamrick and Godt 1990), but few other studies compared populations growing in such close proximity in the same habitat.

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THE EFFECT OF CLIMATIC VARIABILITY ON GROWTH, REPRODUCTION, AND POPULATION VIABILITY OF A SENSITIVE SALT MARSH PLANT SPECIES, *LASTHENIA GLABRATA* SUBSP. *COULTERI* (ASTERACEAE)

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ABSTRACT

As with many other sensitive species in California, the range of *Lasthenia glabrata* Lindley subsp. *coulteri* (A. Gray) Ornd. (Asteraceae; Coulter's goldfields) has been dramatically reduced in recent decades by urbanization. Many populations are small, isolated, and seemingly unstable. In this study, we conducted an autecological assessment of a small *L. glabrata* subsp. *coulteri* population at San Diego County's San Dieguito Lagoon, using a large population at San Elijo Lagoon for comparison. The large population was not only more stable based on trends in seed production, but generally produced larger plants and more flowers and capitulescences than the small population. However, this relationship appears to be temporally variable and influenced significantly by climatic conditions, particularly rainfall totals and distribution. In a year with above-average rainfall, vegetative and reproductive yield of plants in the small population (San Dieguito Lagoon) matched or even exceeded that of plants in the large one (San Elijo Lagoon), which was subjected to prolonged inundation following heavy rains and a back-up of runoff and creek flows behind a dike system. Rainfall is linked not only to soil moisture, but to nutrient influx and cycling, variables that were strongly associated with group (marsh/monitoring year) separation and prediction in statistical analyses. When resources are sufficient, reproductive yield appears to be driven by other factors, the most probable of which is pollen supply. The relationship between rainfall and plant yield could prove integral to predicting long-term viability of *L. glabrata* subsp. *coulteri* populations, as above-average rainfall years are often sporadic and interspersed between lengthy periods of average or below-average rainfall in southern California. Conservation and enhancement of the remaining coastal salt marsh *L. glabrata* subsp. *coulteri* populations could perhaps be furthered by factoring this relationship into conservation and restoration projects and hydrologic regimes designed for managed wetland systems.

Small populations of rare plant species face many genetic, demographic, and ecological challenges. Small populations can suffer from reduced "fitness," often undergoing one or more genetic bottleneck events that reduce genetic variation (Nei et al. 1975; Hamrick et al. 1979; Hedrick 1983; Ledig 1986; Barrett and Kohn 1991 and others). Fewer numbers also create a greater chance for normally outbreeding species to inbreed and become less fit through concentration of deleterious alleles (Charlesworth and Charlesworth 1987 and others). Opportunities for gene flow between populations—and the potential for infusion of new alleles—may be minimal due to the dwindling number of populations and the distance between them. Small plant populations are intrinsically less appealing to pollinators (Powell and Powell 1987; Morgan 1999), which can further reduce fecundity and the potential for even limited outbreeding between more distant individuals. Reduced genetic variation can also increase small populations' susceptibility to herbivory, pathogens, and stochastic factors such as floods and environmental and demographic variability (Shaffer 1981). In addition, population viability can be continually jeopardized by human-related disturbances or changes in watershed or ecosystem conditions—sometimes the very changes believed to have made the species rare in the place. Even efforts to better manage, enhance, or restore systems in which rare plants occur can pose a threat if these activities do not balance their ecological requirements with those of other target plant and wildlife species and the ecosystem as a whole.

Determining whether small populations are succumbing to these challenges is not an easy task. Annual censuses are not only difficult, but often misleading unless conducted over several decades due to cryptic life history stages (i.e., seed banks) and normal fluctuations in population size that may have little impact on population stability or viability (Davy and Jefferies 1981; Schemske et al. 1994; Pavlik 1994 and others). A life table or population viability analysis (PVA) is often considered the optimal approach for assessing population stability (Schemske et al. 1994; Pavlik 1994; Menges 1986). However, the probability of a long-lived seed bank immeasurably complicates performance of a life table or PVA for plant species (Pavlik 1994), despite arguments that there are ways to circumvent calculation of this unknown (Menges 1986). Some alternative approaches to assessing population stabil-

ity involve performance of non-integrated demographic trend assessment, which focuses on overall trajectories in survivorship, seed production, density of viable seed, and frequency of establishment (Pavlik 1994). Morphological attributes associated with productivity or yield such as plant size/biomass and flower number may be incorporated, as well (Menges 1986; Menges and Gordon 1996). These analyses are often improved through using either weedy congeners or large, more stable populations of the same species for comparison (Pavlik 1994).

Consistent with the major role that extrinsic disturbances or changes can play in population viability, many studies on rare species include an ecological, as well as demographic, component (Schemske et al. 1994). Some have criticized researchers for emphasizing autecology over demography in sensitive plant research, characterizing ecological research as premature in the absence of demographic information relevant to population vital rates (Schemske et al. 1994). However, managers of reserves and enhancement/restoration projects often seek ecological information that might help them better manage reserves or design projects (Pavlik 1994). Moreover, ecological data can greatly complement demographic assessments, particularly when the information is integrated to allow for identification of ecological constraints on key life history stages and variables associated with productivity (e.g., plant size, flower number) (Schemske et al. 1994; Pavlik 1994; Menges and Gordon 1986).

San Dieguito Lagoon in San Diego County supports a small population of a rare plant, *Lasthenia glabrata* Lindley subsp. *coulteri* (A. Gray) Ornd. (Asteraceae: Coulter's goldfields). For a sensitive species, *L. glabrata* subsp. *coulteri* has a remarkably diverse distribution. This annual is found in alkali playas in southern California's arid inland areas and salt marshes and vernal pools in the region's more moderate coastal areas (NDDB 1998; Skinner and Pavlik 1994; Hickman 1993).

This diverse distribution has not spared the species from the threat of extirpation, however. All of these habitats have been negatively impacted to some extent by California's extensive urbanization over the past 50 y (Skinner and Pavlik 1994). More than 90 percent of California's wetland habitats, including marshes, vernal pools, and alkali playas, have been destroyed by commercial and residential development, and despite regulatory efforts at effecting a "no net loss" policy, this downward trend in wetland habitat acreage appears to be continuing. The wetland habitats that remain are often fragmented, highly disturbed, and heavily impacted by outside influences such as nutrient and contaminant influx associated with watershed development. The toll these habitat losses and impacts has taken is apparent from the constriction of the species' historic range. In recent decades, its once extensive distribution throughout southern California has been reduced to a few marshes and vernal pools in San Diego, Ventura, and Santa Barbara counties and alkali playas in Riverside County (NDDB 1998).

This precipitous decline in distribution prompted listing of *L. glabrata* subsp. *coulteri* as a species of concern (formerly C2) by the U.S. Fish and Wildlife Service and a species of limited distribution (List 1B) by the California Native Plant Society (CNPS). While its cousin, *Lasthenia glabrata* Lindley subsp. *glabrata,* is relatively common and has even a larger range than subsp. *coulteri,* other *Lasthenia* species that occur in vernal pool habitats such as *Lasthenia burkei* (E. Greene) E. Greene (Burke's goldfields) and *Lasthenia conjugens* E. Greene (Contra Costa goldfields) are faced with similar threats in terms of potential extirpation (Skinner and Pavlik 1994). Within its historic coastal range, *L. glabrata* subsp. *coulteri* often grows in high elevation areas of salt marshes—or the "high marsh"—alongside another sensitive species, *Cordylanthus maritimus* Benth. subsp. *maritimus* (salt marsh bird's beak), a state- and federally listed endangered species.

San Dieguito Lagoon is one of six San Diego County coastal marsh systems that supports historical and/or possibly reintroduced populations of *L. glabrata* subsp. *coulteri.* The species was once present at 10 San Diego County marshes (NDDB 1998), but probably in low abundance, as an early ecological study characterized it as only an "infrequent" inhabitant (Purer 1942). Of the six remaining occurrences, three are believed to be small and relatively unstable populations, including the one at San Dieguito Lagoon. Over the past few decades, *L. glabrata* subsp. *coulteri* numbers at San Dieguito Lagoon have ranged from as low as zero in 1980 (Sea Science Services and Pacific Southwest Biological Services, Inc. 1980) and six in 2000 (Andrea Thorpe personal communication) to as high as 1000 individuals during the mid- and late-1990s (MEC Analytical, Inc. 1993; L. Parsons and A. Whelchel, personal observation). Neighboring marshes such as San Elijo Lagoon, as well as reportedly Los Penasquistos Lagoon, support annual populations consistently numbering as many as 5000 to 10,000 individuals (L. Parsons and A. Whelchel personal observation).

San Dieguito Lagoon is also one of seven coastal marshes in San Diego County, CA, for which restoration and/or enhancement activities have been or are being conducted or are proposed. As with other San Diego County marshes, this coastal lagoon has been subject to a number of historic watershed changes and disturbances, including damming of its river, agricultural and residential development, diking, and intermittent mouth closures that impound water and create hypoxic conditions. With restora-

tion and enhancement plans for San Dieguito La-
goon currently being developed, there appeared to
be a strong and immediate need for information on
demographic and ecological aspects of this small
and possibly unstable population and its potential
for conservation and even future enhancement. Few
studies have actually assessed demography or aut-
ecological relationships of this or other *Lasthenia*
species. The research that exists deals primarily
with upland species (*Lasthenia californica* Lindley;
Rajakaruna and Bohm 1999; Vivrette 1999) or fo-
cuses on salinity tolerance (*L. glabrata* subsp. *coul-
teri;* Kingsbury et al. 1976; Callaway et al. 1990;
Callaway and Sabraw 1994).

In 1996, a study was implemented to assess de-
mographic and ecological characteristics of the *L.
glabrata* subsp. *coulteri* population at San Dieguito
Lagoon. For purposes of performing a comparative
assessment, we broadened the scope of our study
to include another *L. glabrata* subsp. *coulteri* pop-
ulation that appeared to be larger and more stable
in terms of plant numbers, the population at San
Elijo Lagoon, located directly north of San Diegui-
to Lagoon. Through this study, we hoped to gain
insight into differences in survivorship, reproduc-
tive potential (plant size, flower number) and suc-
cess (seed set and seed production) between pop-
ulations. When possible, we also attempted to track
trends in demographic results for purposes of as-
sessing population stability. By comparing autecol-
ogy of a small and unstable population with that of
a large and stable one, we hoped to increase our
understanding of the biotic and abiotic factors that
might be influencing variations in plant yield and
population viability. We believe that this informa-
tion could prove invaluable to resource managers
charged with planning or implementing complex
restoration or conservation projects, particularly
projects with multiple species and ecosystem ob-
jectives.

Study area. San Dieguito Lagoon is located in
Del Mar, CA, approximately 25 km north of San
Diego (Fig. 1). The lagoon's principal source of
freshwater is the San Dieguito River, which has
been dammed to create Lake Hodges, a reservoir
in the inland area of the San Diego County. Water-
shed of the lagoon totals 897 km^2, 785.2 km^2 of
which is behind dams (California Wetlands Infor-
mation System 1996). During the summer and fall,
the lagoon mouth sometimes closes for several
weeks to a month until it re-opens either naturally
or manually (i.e., using bulldozers). Vegetation
communities occurring within the lagoon include
salt and brackish marshes and, at its eastern end,
freshwater marsh and limited riparian habitats. Ap-
proximately 104 of the 240 hectares of wetlands
once present at San Dieguito Lagoon still remain
(California Wetlands Information System 1996). In
addition to damming, the watershed of the lagoon
has been altered considerably by development of
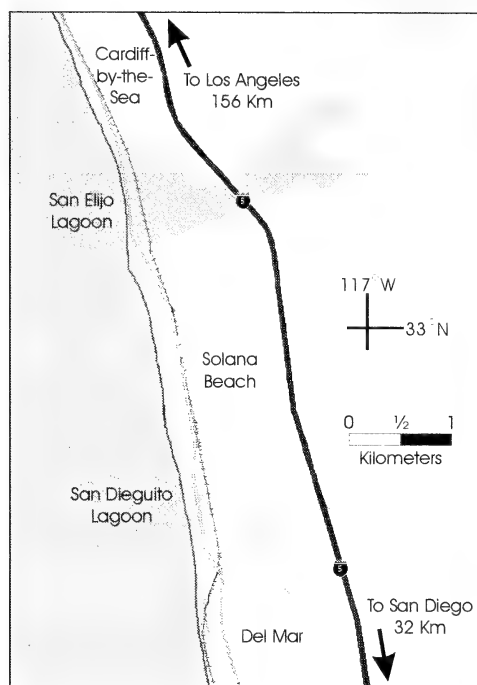
FIG. 1. Location of *Lasthenia glabrata* subsp. *coulteri*
(Coulter's goldfields) study areas in San Diego County,
CA.

the adjacent floodplain and uplands for agriculture,
commercial and residential structures, and a race-
track/fairgrounds. The population of *L. glabrata*
subsp. *coulteri* at this lagoon is located in a muted
tidal basin in the southern portion of the lagoon,
approximately 2 km from the mouth.

San Elijo Lagoon is located in the Cardiff, CA,
approximately 27.5 km north of San Diego and di-
rectly north of San Dieguito Lagoon (Fig. 1). Sev-
eral creeks flow into the lagoon, one of which is
dammed by Lake Wohlford (Escondido Creek). The
watershed for San Elijo Lagoon is 200.2 km^2 (Cal-
ifornia Wetlands Information System 1996). The
mouth of San Elijo Lagoon also closes during the
summer and fall, typically with more frequency and
longer duration than San Dieguito Lagoon. Current
wetland acreage at San Elijo Lagoon totals 230.4
ha and is comprised of salt marsh, brackish marsh,
freshwater marsh, and riparian habitat (California
Wetlands Information System 1996). The water-
shed of this lagoon has been altered considerably
by development of the adjacent floodplain and up-
lands for farming and commercial and residential
structures. The lagoon has also been separated into
a series of hydrologic "cells" by construction of
a series of dikes and levees between 1880 and
1940. By closing flood gates at one of the eastern
dikes, the area east of Interstate 5 is partially
flooded from November through March for water-
fowl enhancement (Susan Welker personal com-
munication). The population of *L. glabrata* subsp.

TABLE 1.   MEAN ANNUAL TEMPERATURE AND RAINFALL AND NUMBER OF DAYS THAT LAGOON MOUTH WAS OPEN DURING THE STUDY PERIOD (1996–1999).

| Year end | San Diego NWS-Lindbergh (NOAA; CDWR) | | | | San Dieguito Lagoon | | San Elijo Lagoon | |
	Temperature (Jan–Dec) mean (deg.C)	Departure from mean (% of mean)	Rainfall (Oct–April) total (cm)	Departure from mean (% of mean total)	No. of days mouth open* (Nov–Oct)	% of year	No. of days mouth open** (Nov–Oct)	% of year
1996	17.8	99.4	12.85	53.4	351	96	80	22
1997	18	100.5	17.48	72.7	358	98	153	42
1998	18.5	103.4	42.75	177.8	338	92	238	65
1999	15.6	87.2	16.2	67.4	219***	60	240	66

NOAA = National Oceanic Atmospheric Administration Center, National Climatic Data Center
CDWR = California Department of Water Resources, California Data Exchange Center, CIMIS
* = H. Elwany, unpublished data; San Diego County Department of Environmental Health
** = San Diego County Parks Department, unpublished data
*** = All closure events occurred after April 1999 and plant senescence

coulteri at this lagoon occurs at the eastern end of the lagoon in an area that receives little to no direct tidal flow, although some subsurface tidal inflow may occur.

Mean annual temperature and rainfall data and data for the number of days the lagoon mouths were open for the study period (1996–1999) are provided in Table 1. Rainfall was 53 to 73 percent of average during October–April in 1996, 1997, and 1999 and 178 percent of average during those months in 1998. Annual mean daily temperature showed less variation (87 to 103 percent of average between 1996–1999).

METHODS

Annual Monitoring

Demography. In general, demographic information was collected in 1996, 1997, 1998, and 1999 at San Dieguito Lagoon and in 1997, 1998, and 1999 at San Elijo Lagoon. To assess demography, 14 plants within each of 10 sampling locations (0.5 × 0.5 m plots) were haphazardly chosen and marked in late January or early February of each monitoring year, when the plants were 1 to 2 cm tall seedlings. The sampling locations were chosen as representative of the microhabitat diversity and environmental heterogeneity present with the populations' existing range at each marsh. Mortality and phenology were assessed on a monthly or twice monthly basis for three months: February, March, and April. Mortality was assessed as the number of marked plants that died between marking and mid-April. Phenology was broken into three basic stages: vegetative, in bud, and flowering. In addition, plants were examined for signs of potential herbivory. In mid-April, when most plants had already set seed, a minimum of 10 plants and a maximum of 14 plants were harvested from each sampling location to determine aboveground plant height (cm), number of capitulescences (inflorescences), capitulescence diameter (the diameter of

the receptacle in mm excluding ray flowers), number of flowers (total of disc and ray flowers), number of seeds, and seed set (number of seeds/number of flowers). Seeds were also examined for signs of granivory or seed predation.

There were some exceptions to the described demographic monitoring. Mortality was not assessed during the following marsh/years—San Dieguito Lagoon 1996 and 1999 and San Elijo Lagoon 1999—but plants were harvested in mid-April for measurement of plant height, capitulescence number and diameter, flower and seed number, and seed set. Efforts were made to assess survivorship at San Dieguito Lagoon and San Elijo Lagoon in 1998, but a sedimentation event associated with higher-than-average water levels in the study area at San Elijo Lagoon caused marking materials (colored rubberbands) to be obscured. The 1998 data for San Dieguito Lagoon was incomplete, as information on mortality was not collected in April.

Biotic variables. Density of *L. glabrata* subsp. *coulteri* was assessed biweekly in 1997 using a 0.5 × 0.5 m quadrat subdivided into 25 1-dm^2 subquadrats. One of the subquadrats was randomly chosen, and the number of *L. glabrata* subsp. *coulteri* individuals present within the subquadrat was counted. Also, vegetative cover within the sampling plot was assessed one time per monitoring year using the 36 cross points of the subdivided 0.5 × 0.5 m quadrat and recording the species or bareground occurring below the cross point. For analysis purposes, percent cover was calculated for *L. glabrata* subsp. *coulteri,* total vegetation cover, and cover of non-native species. Total vegetation cover included both native and non-native species. Native species were primarily coastal salt marsh inhabitants such as *Salicornia virginica* L. (pickleweed), *Salicornia subterminalis* Parish (glasswort), *Frankenia salina* (Molina) I. M. Johnston (alkali heath), *Cressa truxillensis* Kunth (alkali weed), and *Spergularia marina* (L.) Grisels. (sand-spurrey). Non-native spe-

cies included *Cotula coronopifolia* L. (brass-buttons), *Mesembryanthemum crystallinum* L. (crystalline iceplant), *Lolium multiflorum* Lam. (Italian ryegrass), *Parapholis incurva* (L.) C. E. Hubb. (sickle grass), *Polypogon monspeliensis* (L.) Desf. (annual beard grass), and *Poa annua* L. (annual bluegrass).

Abiotic variables. A total of 11 abiotic variables was assessed during each monitoring year, except 1999. The abiotic variables were soil pH, soil salinity, soil moisture, organic matter, ammonium, nitrates + nitrites, phosphorous, cation exchange capacity (CEC), calcium, magnesium, and potassium. Soil texture was assessed at both marshes in 1997. As this species grows in high marsh areas, which are only infrequently inundated, reduction-oxidation potential was not measured. Soil pH, soil salinity, and soil moisture was measured twice a month (1997) to monthly (1998) from 15-cm-deep soil core samples at all 10 sampling locations. Soil pH was measured by creating soil pastes in the field and measuring with an Oakton phTestr 3 (±0.01 pH resolution) field pH probe. Soil salinity was measured by expressing soil water from a syringe fitted with filter paper onto a refractometer, which reports salinities in grams per kilogram. Soil moisture was measured by removing 10- to 15-cm soil cores and assessing loss of mass on drying (Gardner 1986). For nutrient analysis, five of the 10 sampling locations at each marsh were randomly selected for subsampling twice each monitoring year (mid-February and mid-March). At these subsampling locations, approximately 100 g of soil was removed, air dried, and sent to A&L Western Agricultural Laboratories (Modesto, California) for measurement of organic matter, ammonium, nitrates + nitrites, phosphorous, cation exchange capacity, calcium, magnesium, and potassium. In 1997, the laboratory also analyzed soil texture. The procedures described above were performed for both marshes during the years monitoring was performed, with the exception of San Dieguito Lagoon in 1996 and 1999 and San Elijo Lagoon in 1999. Soil salinity was not measured at San Dieguito Lagoon in 1996, and pH, soil moisture, organic matter, and other nutrients were only analyzed once during the 1996 monitoring year. Data for variables sampled more than once per season were averaged for analysis.

Data analysis. Differences in plant population dynamics between marshes and sampling years were assessed by treating each "marsh/year" sampled independently and conducting a One-Way Analysis of Variance using the Systat computing package (SPSS, Chicago, IL). For the density comparison, a t-test was conducted to test for differences in plant density between marshes. When assumptions for parametric tests were not met, data were either transformed, or an equivalent, non-parametric procedure (e.g., Kruskal-Wallis) was

conducted. If a significant difference was found, differences between particular means were analyzed further by using either Tukey, T'-method (Sokal and Rohlf 1981), or non-parametric Tukey-type (Zar 1984) multiple comparison procedures. The dependent variable plant height was log-transformed for analysis.

Discriminant function analysis was used to explore the association between plant population dynamics and 13 biotic and abiotic factors within marshes. Quadratic discriminant function analyses were performed, because they are less sensitive to dissimilarities in covariance matrices between groups. Groupings used in analyses were based on results from the Analysis of Variance tests, with generally low yield plots separated from high yield plots. The analyses incorporated data from 1996–1998: no biotic and abiotic data were collected in 1999. As salinity data were not available for San Dieguito in 1996, a preliminary analysis was performed using models that incorporated the salinity variable, but not the San Dieguito 1996 data. If salinity did not have a strong loading on any canonical variable, a second or final analysis was performed using models that incorporate San Dieguito 1996 data, but not the salinity variable. For the reproductive success analyses in which groups were smaller, fewer than 13 variables were incorporated, using F-to-enter from the preliminary analyses as the criterion. Discriminant function analyses were conducted using the Systat computing package. The following variables were log transformed for analysis: ammonium, nitrate + nitrite, calcium, and cation exchange capacity.

RESULTS

Comparison of plant yield between marshes. One of the intents of our study was to compare attributes of a small, and perhaps unstable, population with those of a large and stable one. A component of this study involved assessment of demographic variables associated with survivorship and yield to determine the degree to which these populations actually differ other than in estimated population size. As shown in Figure 2, there were statistically significant differences between marsh/years for mean survivorship (per 0.25 m² plot; ANOVA, F = 8.67, n = 30, P = 0.001), mean plant height (ANOVA, F = 56.8, n = 69, P < 0.001), mean capitulescence number (Kruskal-Wallis, Test Stat. = 46.3, n = 69, P < 0.001), mean capitulescence diameter (ANOVA, F = 19.6, n = 69, P < 0.001), mean flower number (Kruskal-Wallis, Test Stat. = 28.5, n = 49, P < 0.001), mean number of seeds produced (seed number) (Kruskal-Wallis, Test Stat. = 54.3, n = 69, P = 0.001), and mean seed set (mean number of seeds/mean number of flowers) (ANOVA, F = 25.1, n = 49, P < 0.001). The mean percent cover of *L. glabrata* subsp. *coulteri* within 0.25m² sampling plots also differed between marsh/years
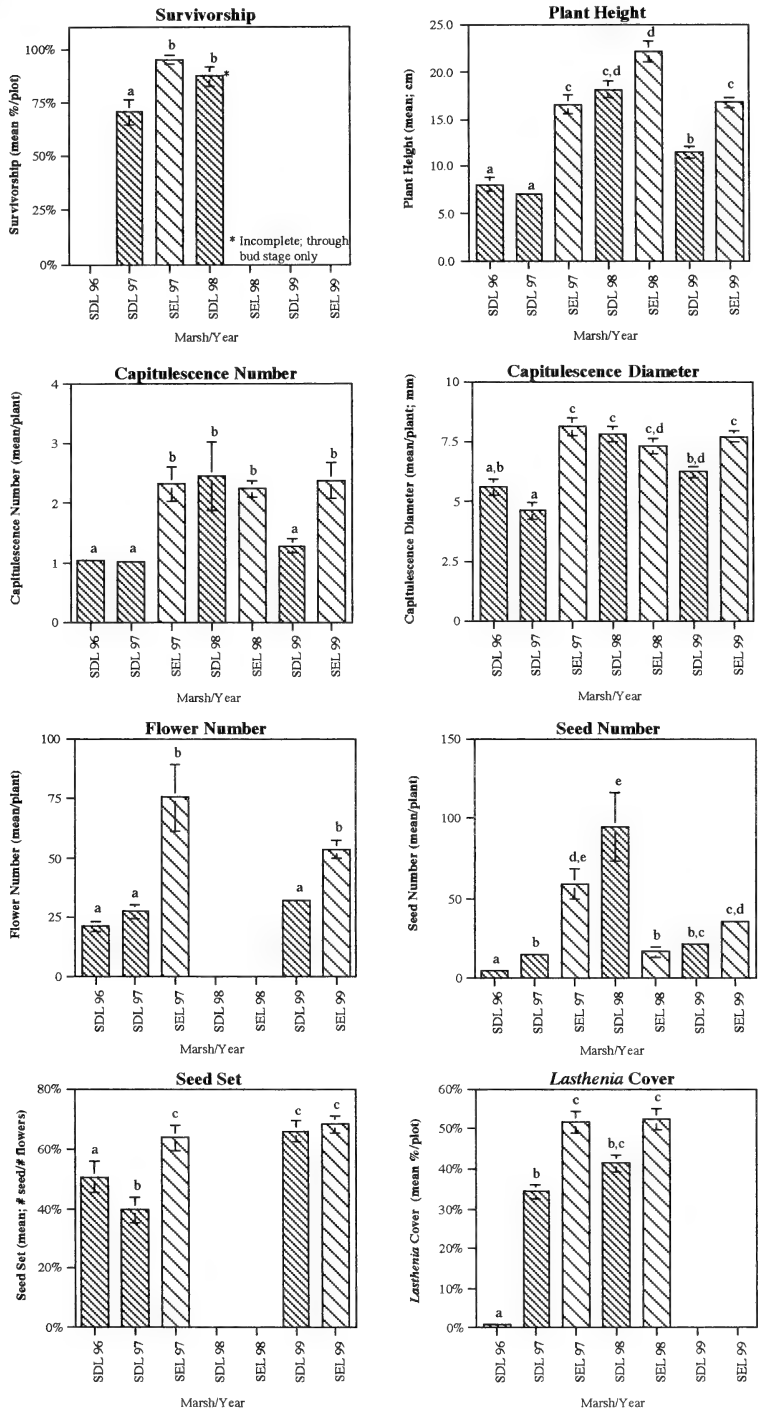
FIG. 2.   Means for dependent plant variables in marsh/years studied. Differences between marsh/years were significant for all analyses (P for all ANOVA/Kruskal-Wallis = or < 0.001). Differences between particular means are indicated by small case letters. Bars represent plus or minus 1 SE (standard error): means seemingly without bars are ones with very small standard errors. Plot refers to individual sampling plots, which were 0.25 m² in size.

(Kruskal-Wallis, Test Stat. = 26.12, n = 49, P < 0.001). Measurements of these variables were not assessed for all marsh/years. Specifically, survivorship data were only available for three marsh/years, and survivorship for San Dieguito Lagoon 1998 was assessed only through bud stage. Data for mean flower number, mean seed set, and cover of *L. glabrata* subsp. *coulteri* were only available for five marsh/years.

Closer examination of the results and multiple comparison tests reveals some interesting trends. Survivorship through the vegetative stage was lower at San Dieguito Lagoon 1997 than at San Elijo Lagoon 1997 and San Dieguito Lagoon 1998 (Fig. 2). However, despite these statistical differences, seedling survivorship at both marshes remained generally high (>70 percent). Based on biweekly censuses for marked individuals, most mortality occurred just prior to or after reproduction. In 1997, total survivorship at reproductive maturity (flowering stage) was 72 percent for San Dieguito Lagoon and 95 percent for San Elijo Lagoon. As the San Dieguito Lagoon population matured more quickly than San Elijo Lagoon, it is probable that some of the mortality occurred after reproduction and therefore actually constituted senescence. The results suggest that, at least in 1997, the populations were following the Deevey Type I survivorship curve characteristic of stable populations (Pavlik 1994), in that the mortality inflection point followed onset of seed production. Furthermore, as the data for San Dieguito 1997 was recorded during a below-average rainfall year, low mortality cannot necessarily be ascribed to above-average environmental conditions.

Means for plant height, capitulescence diameter and number, and flower number also showed some interesting relationships. Means were not only generally lower at San Dieguito Lagoon than at San Elijo Lagoon, but remarkably similar between years within the respective marshes. There was one exception. In 1998, yield of the San Dieguito Lagoon plants was actually closer to that of the 1997, 1998, and 1999 San Elijo Lagoon plants. Means for plant height and capitulescence diameter suggested that San Dieguito Lagoon 1999 might be intermediate between low and high yield marsh/years, but those for capitulescence and flower number were equivalent to means in low yield years.

Results for seed set and seed number were somewhat more complex. Plants at San Dieguito Lagoon set less seed in 1997 than in 1996, and seed set (number of seeds/number of flowers) was lower in both of these marsh/years than in San Dieguito Lagoon 1999 and San Elijo Lagoon 1997 and 1999. For the total number of seeds produced, however, the 1996 San Dieguito Lagoon marsh/year was the least productive. The distinction between the remaining marsh/years was less clearcut, but in terms of seed productivity, the ranking appeared to be, from lowest to highest, as follows: San Dieguito

Lagoon 1997 and San Elijo Lagoon 1998; San Dieguito Lagoon 1999; San Elijo Lagoon 1999; San Elijo Lagoon 1997; and San Dieguito Lagoon 1998. Unlike the 1997 survivorship data, these results suggest that the San Dieguito Lagoon population might be less stable than that of the larger San Elijo Lagoon one. Based on non-integrated demographic trend analysis, seed production per individual of stable populations should consistently equal or exceed that of a common congener or more stable population (Pavlik 1994). With the exception of 1998, seed production of the San Dieguito Lagoon plants was typically lower than those at San Elijo Lagoon. The large differences observed in annual population size may have only exacerbated this disparity in seed production between populations.

Plant yield and influence of biotic and abiotic factors. The dissimilar patterns in sample means observed for mean seed number and seed set and the other plant variables may relate to an underlying difference in how biotic and abiotic factors affect various stages or aspects of plant development. Based on these patterns, we decided to analyze our results by dividing our results into two grouping structures—reproductive potential and reproductive success. Reproductive potential measures the potential of the plant to be more reproductively successful through survivorship to reproduction (mortality), being larger (mean plant height), and producing more capitulescences (mean capitulescence number) and more flowers (mean capitulescence diameter and mean flower number). All of these variables relate to an individual's ability to outcompete another in terms of attracting pollinators or utilizing limited resources (e.g., water, nitrogen, etc.). Reproductive success measures the actual success of an individual in reproducing, as determined by seed number and seed set (percentage of flowers producing seed).

For dependent variables such as plant height, capitulescence diameter and number, and flower number, marsh/years generally split into two groups based on yield, with San Dieguito Lagoon 1996, 1997, and 1999 in a low yield group (Reproductive Potential 1/RP1) and San Dieguito Lagoon 1998 and San Elijo Lagoon 1997, 1998, and 1999 in a high yield group (Reproductive Potential 2). For the dependent variables seed number and seed set, groupings were less distinct, but marsh/years were separated into three groups, with San Dieguito Lagoon 1996 in a low yield group (Reproductive Success 1/RS1), San Dieguito Lagoon 1997 and San Elijo Lagoon 1998 in an intermediate yield group (Reproductive Success 2/RS2), and San Elijo Lagoon 1997 and 1999 and San Dieguito Lagoon 1998 and 1999 in a high yield group (Reproductive Success 3/RS3).

Reproductive potential of a germinated seedling is typically affected by herbivory, environmental factors, and intra- and inter-specific competition.

Herbivory can negatively affect individuals through consumption of either vegetative tissue or flowers, which may weaken or kill the plant. Through the three years of study, no herbivory of vegetative tissue or flowers was observed at either marsh. The effect of intra- and inter-specific competition is not as directly observable and can be more complicated. At high intra- or inter-specific densities, seedlings can compete for resources or light or become more attractive to herbivores. At later stages, however, high densities of synchronously flowering individuals, including non-native neighbors such as *Cotula coronopifolia,* may also serve to attract pollinators and thereby enhance reproductive success.

Some estimates of *L. glabrata* subsp. *coulteri* density were collected in 1997, and densities ranged from three individuals (San Elijo Lagoon) to 140 individuals (San Dieguito Lagoon) per dm². Overall, the 1997 sampling plots at San Dieguito Lagoon had higher densities per dm² (71.6 ± SE 13.5) than those at San Elijo Lagoon (28.4 ± SE 7.2) (*t*-test, $t = 2.83$, n = 20, P = 0.011). Densities of other species were not estimated, but cover of other native species ranged from 0 to 75 percent, and cover of non-native species ranged from 0 to 50 percent. Extremely low total mortality rates for vegetative and flowering individuals at both marshes in 1997 (~72 to 95 percent) suggests that either abundance of *L. glabrata* subsp. *coulteri* or other species was not high enough, or resources not limited enough, to have induced either intra- and inter-specific competition at the seedling or vegetative stage during this year. While above-average rainfall may have increased seedling densities at San Dieguito Lagoon in 1998, the fact that 89 percent of the plants reached at least bud stage suggests that densities were not high enough to incur density-dependent mortality.

Reproductive success is affected by all the same factors as reproductive potential, but other factors can limit reproduction, as well, specifically granivory (herbivory of unfertilized ovules or seed) and, for non-vegetative species such as *L. glabrata* subsp. *coulteri,* pollination success. Based on statistical analyses, reproductive success was highest for the RS3 group (San Elijo Lagoon 1997 and 1999 and San Dieguito Lagoon 1998 and 1999) and lowest in the RS1 group (San Dieguito Lagoon 1996). The fact that marsh/years with technically equivalent reproductive potential (San Dieguito Lagoon 1996 and 1998) should have differing rates of reproductive success suggests that a different factor or suite of factors may be affecting seed number and seed set.

As noted earlier, no consumption of entire flowers was observed during the three years of study, and low mortality rates indicate that most individuals survived to flowering and seed set. It is possible that competition among individuals for resources increased during the flowering stage, as ambient temperatures and rates of evaporation and evapotrans-

piration typically climb during the warm spring months. Flowering often coincides with a neap tide series, a period of extremely low tides that often decrease soil moisture and increase evaporation rates and soil salinity in higher marsh elevations.

Some granivory was actually observed in seeds of San Dieguito Lagoon individuals in 1998. The extent of granivory was not quantified, but in general, the number of individuals and/or number of seeds per individual that appeared to have been affected was relatively low. While viability of the damaged seeds was not tested, the damage appeared extensive enough to render the seeds inviable. Granivory, or pre-dispersal predation, was not observed in the other study years at this marsh, nor was it observed in seeds of plants from San Elijo Lagoon. The presence of organisms that would remove seeds after dispersal, including ground-dwelling insects such as ants, was sporadic, and even when present, abundance was low. Ground-dwelling organisms observed within *L. glabrata* subsp. *coulteri* patches included ants (Formicidae), thrips (Thysanoptera), and rove (Staphylinidae) and other beetles (*Bembidion* sp. and Dermestidae) (Wesley Maffei personal communication). With the exception of ants, these invertebrates are considered unlikely post-dispersal seed predators. None of these organisms, including the ants, were observed removing fallen seeds, nor were birds observed foraging in these areas.

Pollination was not included within the scope of our study, but many insects were observed visiting flowers during our sampling efforts. The primary insect visitors appeared to be solitary bees (*Andrena pallidofovea* and A. *cercocarpi*), beetles (Dermestidae, *Geocoris* sp.), beeflies (Bombyliidae), flies (*Bufolucilia* sp. and *Nemotelus* sp.), butterflies (*Coenonympha californica*), and halictine or "sweat" bees (*Lasioglossum* sp.) (W. Maffei personal communication; Robbin Thorp personal communication). Several of these visitors have the potential to effect pollination either through collecting pollen (e.g., Andrenidae or halictine bees) or foraging on pollen or other flower parts (e.g., Dermestidae). Overall, visitor numbers and species diversity appeared to be lower at San Dieguito Lagoon than at San Elijo Lagoon, although no formal pollinator observations were conducted.

Based on these observations, we hypothesize that resources such as nutrients and perhaps even pollen may be the primary determinants or reproductive potential and success.

Discriminant function analysis. To explore further the association between biotic and abiotic factors and the groupings of marsh/years suggested by results of multiple comparison testing, discriminant function analyses were performed. The question posed by these analyses was two-fold. Using the groups suggested by multiple comparison testing, was there some combination of biotic and abiotic

TABLE 2. RESULTS OF THE DISCRIMINANT FUNCTION ANALYSES FOR THE REPRODUCTIVE POTENTIAL AND SUCCESS MODELS.

Reproductive Potential Model
Canonical Variable: 0.002*pH − 0.193*organicmatter − 1.330*soilmoisture + 1.092*phosphorous − 0.005*potassium − 0.189*magnesium − 0.443*totalplantcover − 0.406*ammonium_log − 0.113*nitrates + nitrites_log + 0.326*non-nativeplantcover − 0.487*calcium_log − 0.699*CEC_log

Classification results: Actual groups	Results–Cases (%)		Jackknifed Results–Cases (%)	
	RP1	RP2	RP1	RP2
RP1	16(100)	0	15(94)	1(6)
RP2	0	15(100)	0	15(100)
Total % Correct		100		97

Reproductive Success Model
Canonical Variable 1: 0.386*pH − 1.235*soilmoisture − 0.651*organicmatter + 0.937*phosphorous − 0.438*potassium + 0.106*magnesium + 0.422*totalplantcover + 0.756*ammonium_log + 1.406*nitrates + nitrites_log
Canonical Variable 2: 0.482*pH + 0.771*soilmoisture + 0.258*organicmatter − 1.265*phosphorous + 0.421*potassium + 0.786*magnesium + 0.253*totalplantcover + 0.754*ammonium_log + 0.497*nitrates + nitrites_log

Classification results: Actual groups	Results—Cases (%)			Jackknifed Results—Cases (%)		
	RS1 (%)	RS2 (%)	RS3 (%)	RS1 (%)	RS2 (%)	RS3 (%)
RS1	10(100)	0	0	10(100)	0	0
RS2	0	11(100)	0	0	11(100)	0
RS3	0	0	10(100)	0	0	10(100)
Total % Correct			100			100

	Group Means for Models				
	Reproductive Potential		Reproductive Success		
Variables measured	RP1	RP2	RS1	RS2	RS3
pH	7.59	7.83	7.43	7.78	7.90
% Soil moisture	29.6	40.3	25.9	37.2	41
% Organic matter	2.62	3.65	1.84	3.39	4.11
Phosphorous (ppm)	46.1	52.7	39.90	53.41	54.05
Potassium (ppm)	414.6	346.6	425.60	347.86	375.10
Magnesium (ppm)	1036.6	1104.2	1024.60	1030.82	1156.35
% Total plant cover	76.3	64	89.8	65.9	55.7
Log-Ammonium (ppm)	1.15	1.11	1.09	1.09	1.22
Log-Nitrates + Nitrites (ppm)	1.38	1.06	1.68	0.96	1.06
% Non-native plant cover	27	8.5	25.0NI	19.2NI	9.9NI
Log-Calcium (ppm)	3.42	3.76	3.35NI	3.65NI	3.75NI
Log-CEC (meq/100g)	1.75	2.26	1.83NI	2.12NI	2.04NI
Soil salinity (ppt)	58.7NI	33.1NI	NA	38.6NI	42.4NI

NA-Not available; NI-Not included in models (see Methods and/or Results for explanation.)

variables that would allow us to discriminate between these groups? And, if so, what combination of variables would allow us to best predict the group to which the sampling location belonged? Two models were used. One model separated sampling locations into two groups (RP1, RP2) based on differences in sample means for reproductive potential variables, and another separated sampling locations into three groups (RS1, RS2, and RS3) based on differences in sample means for reproductive success variables. The groupings were essentially the same as described previously, except for the absence of San Dieguito Lagoon and San Elijo Lagoon 1999: no biotic and abiotic data were collected in 1999. The 13 biotic and abiotic variables used in the models were: pH, salinity, soil moisture, organic matter, ammonium, nitrates + nitrites, phosphorous, potassium, magnesium, calcium, cation exchange capacity, total vegetation cov-

er, and non-native plant species cover. While soil salinity appeared to be higher for RP1 than RP2 (Table 2), it did not have a strong loading in preliminary analyses for either model or correlation with other variables and was therefore not incorporated into final analyses.

According to the reproductive potential analysis, the biotic and abiotic variables used discriminated well between the groups suggested by multiple comparison results (F = 8.34, n = 31, P < 0.0001). Canonical scores of group means were 2.21 for RP1 and −2.36 for RP2. The canonical discriminant function accounted for approximately 100 percent of the total dispersion in the data. Based on the standardized functions, most of the group separation came from soil moisture, phosphorous, calcium, and cation exchange capacity. The canonical variable and a list of group means is provided in Table 2. Using the canonical variable, the model
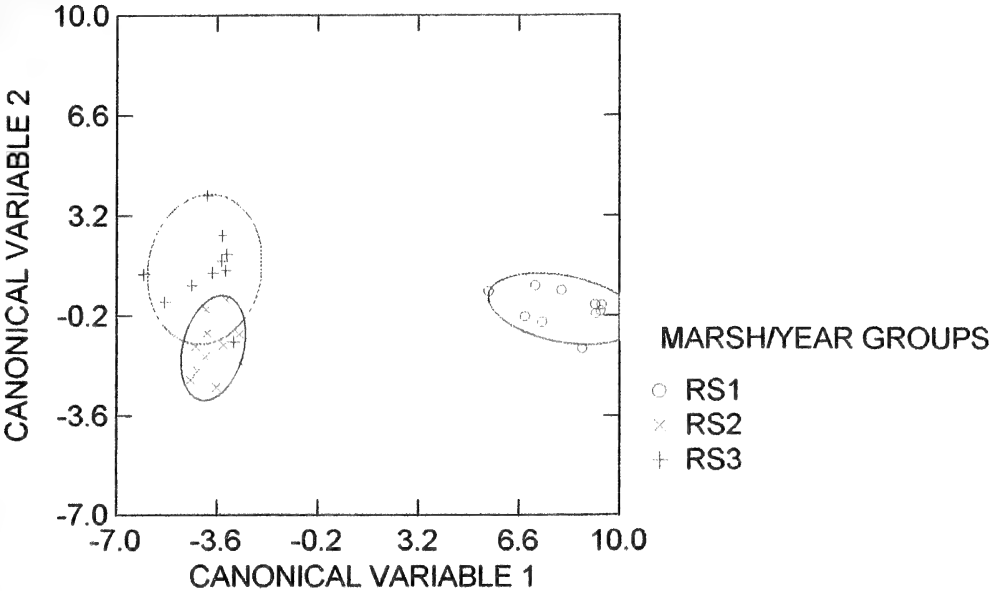
FIG. 3.   Canonical scores plot for the reproductive success model of the discriminant function analysis. Soil moisture and nitrate + nitrite concentrations appeared to provide most of the separation between RS1 and RS2/RS3. Abiotic factors were also able to separate RS2 and RS3, although the separation appeared weaker.

was able to correctly predict or classify sampling locations 100 percent of the time (jackknifed classification matrix = 97 percent).

The reproductive success analysis was also successful at using nine of the biotic and abiotic variables to discriminate between the three groups suggested by multiple comparison results (F = 18.04, n = 31, P < 0.0001; Fig. 3). Canonical scores of group means were (8.09, 0.03) for RS1, (−3.72, −1.29) for RS2, and (−4.00, 1.38) for RS3. The canonical discriminant function, which has two variables, accounted for 100 percent of the total dispersion in the data. The first canonical variable accounted for approximately 96 percent of the data dispersion. The canonical variables and a list of group means are provided in Table 2. As Figure 3 illustrates, most of the group separation comes from the first canonical variable, which appears to split RS1 (San Dieguito 1996) from the other marsh/ years. The first canonical variable had strong loadings for nitrates + nitrites, soil moisture, phosphorous, ammonium, and organic matter. The second canonical variable involved separation of RS2 from RS3, although the degree of separation relative to RS1 appeared weaker. At least three of the sampling locations from RS2 appeared to associate more strongly with RS3, while one of the RS3 locations was grouped with RS2 (Fig. 3). The second canonical variable had strong loadings for phosphorous, magnesium, soil moisture, ammonium, and nitrates + nitrites. Using the canonical variables, the model was able to correctly classify sampling locations 100 percent of the time (jackknifed classification matrix = 100 percent).

The strong separation of marsh/year groups effected by soil moisture, phosphorous, cation exchange capacity, and calcium supports the premise that resources are the primary limiting factors of reproductive potential. Standardized canonical coefficients and group means for soil moisture, cation exchange capacity, and calcium concentrations point to a positive, perhaps even linear, relationship between resource factor and plant variable (Table 2—canonical variable).

The relationship between phosphorous concentrations and L. glabrata subsp. coulteri yield appears somewhat more complicated than that for soil moisture, cation exchange capacity, and calcium concentrations. Standardized coefficients suggest that elevated phosphorous concentrations may actually drive the canonical score toward RP1, which had a low yield. In contrast, group means show highest phosphorous concentrations in marsh/years with the highest reproductive potential. This disparity between group means and standardized coefficients for phosphorous also occurred in the reproductive success model.

As shown in Figure 3, resources also appear to play a role, if perhaps a more limited one, in reproductive success. As hypothesized earlier, the suite of factors influencing vegetative yield appeared to be slightly different from that affecting seed production, which may account for the difference in reproductive success observed between marsh/years with similarly sized individuals (San Dieguito Lagoon 1996 and San Dieguito Lagoon 1997). While soil moisture and phosphorous concentrations featured prominently in both analyses,

nitrogen concentrations (ammonium and nitrates + nitrites) appeared to have a larger effect on reproductive success than on reproductive potential. As was the case with phosphorous, standardized coefficients for nitrates + nitrites and ammonium suggest that elevated concentrations of inorganic nitrogen may actually drive canonical scores toward RS1 and a reduced reproductive yield, although group means for ammonium were marginally higher in RS3 than in either RS1 or RS2. Based on standardized coefficients and group means, only organic nitrogen sources such as organic matter appeared to contribute directly to enhanced seed production.

The evidence for resource limitation of seed production is somewhat weaker for the RS2 and RS3 groups. The reproductive success analysis did provide at least enough separation between RS2 and RS3 using canonical variable 2 to enable successful group differentiation and prediction. As with canonical variable 1 (Table 2), standardized coefficients for phosphorous in canonical variable 2 again appear to drive canonical scoring toward reduced yield, despite the fact that phosphorous concentrations were slightly higher in the group producing the most seeds (RS3). However, in contrast to canonical variable 1, inorganic nitrogen, along with soil moisture and magnesium, appeared to play a positive role in influencing reproductive yield. While the biotic and abiotic factors included in the analysis do enable successful separation between RS2 and RS3, the slight to moderate overlap between groups displayed graphically in Figure 3 suggest that, at some resource level, the number of seeds produced may be driven by other factors not included in this analysis, the most probable of which is pollen supply.

DISCUSSION

Soil moisture would seem an unlikely constraint in a salt marsh, but the high marsh represents a distinct ecotone in an aquatic environment. In general, high marsh species must contend with a complex series of hydrologic cycles: days or even weeks of flooding in the winter may be followed by months where the high marsh or marsh periphery is only inundated or saturated from subsurface flow during the highest high tides. The hydrologic complexity is compounded in managed lagoons, where the lagoon may be flooded deliberately to attract waterfowl or the tidal inlet may remain closed for most of the year even after winter storms elevate internal water levels. In several instances, water or moisture stress has been singled out as a primary factor limiting growth of species in the upper marsh zones (Boorman 1971; De Leeuw et al. 1990). Conversely, too much water or waterlogging can negatively affect species adapted to the typically well-drained soils of the high marsh or marsh periphery (Phleger 1971; Nestler 1977; Parrondo et

al. 1978; Cooper 1982; Seliskar 1985; Adams and Bate 1994).

Waterlogging may account for the anomalous results recorded in 1998, when survival (L. Parsons personal observation) and reproductive yield of the San Elijo Lagoon population plummeted and was significantly less than that of San Dieguito Lagoon. Nineteen ninety-eight was the one year during our study when rainfall was above average (178 percent of average during the months October–April; Table 1). During that year, back-up of run-off and creek flows kept water levels within the eastern area of the lagoon substantially elevated for weeks. In general, reproductive yield of this population was actually highest in the two years where rainfall was slightly below average—1997 (73 percent of average) and 1999 (67 percent of average). In below-average years, the current hydrologic management regime, in which the sluice gates are closed for waterfowl enhancement and outflow is provided through dips in a dike system, may actually enhance the population by artificially maintaining saturated soil conditions within the eastern portion of the lagoon. Conversely, the response of the San Dieguito Lagoon population to rainfall is more consistent with plants being limited by lack of water. Above-average rainfall during 1998 was directly associated with dramatic increases in vegetative and reproductive yield. The positive association between rainfall and yield, combined with the strong evidence of resource limitation in discriminant function analyses, suggests that, at San Dieguito Lagoon, rainfall both directly and indirectly boosts input and cycling of resources such as water and nutrients.

The importance of nutrient limitation in coastal salt marsh plant communities has been well documented (Tyler 1967; Pomeroy et al. 1969; Valiela and Teal 1974; DeLaune et al. 1979; Smart 1982; Long and Mason 1983; Mitsch and Gosselink 1986; Covin and Zedler 1988; Langis et al. 1991; Parsons and Zedler 1997; Boyer and Zedler 1988 and 1999). Our results generally show that higher yields are linked to higher nutrient concentrations. The seemingly negative relationship between phosphorous and inorganic nitrogen concentrations and plant yield observed in analyses could have resulted from some indirect effect of nutrient influx, such as greater competition with more abundant species for light, moisture, or nutrients (Bollens et al. 1998). However, neither total plant cover or cover of non-native species factored strongly into the discriminant function analyses. Based on group means showing elevated levels of phosphorous and, to some extent, ammonium in high yield plots (Table 2), it is more probable that these nutrients must interact with other resource variables in such a way that yield is maximized in areas with moderate concentrations of phosphorous and inorganic nitrogen. If such an interaction exists, our analyses were not sensitive enough to detect it, as no strong correla-

tion was evident between biotic and abiotic dependent or predictor variables (correlation <71 percent).

In general, plasticity in growth or reproduction in relation to rainfall and changes in soil moisture and nutrient input should be expected in annual plant species within Mediterranean climates, even in aquatic systems such as salt marshes. These opportunistic life forms must rely almost entirely on nature's largesse to propagate, survive, and succeed as they have none of the mechanisms (e.g., deep taproots, strongly developed mycorrhizal associations, waxy cuticle layer on leaves, etc.) that enable perennial plants to cope with drought and other climatic challenges. Several studies on salt marsh annuals, including an occurrence of *L. glabrata* subsp. *coulteri* at Carpinteria Marsh near Santa Barbara, California, have linked above average rainfall to increases in relative abundance (Allison 1992; Parsons and Zedler 1997) and density, distribution, and biomass (Callaway and Sabraw 1994). Terrestrial species are also strongly influenced by soil moisture (Reynolds et al. 1997; Center for Conservation Biology 1994), with yield for grassland members of *Lasthenia* such as *L. californica* optimized both during wet years and when growing in wet microsites (Hobbs and Mooney 1991, 1995). For perennial species, the effect of below average rainfall may be more subtle than for annuals, though no less significant, resulting in substantial reductions in seed set (Morgan 1999) and ultimately recruitment and population growth rates (Maschinski et al. 1997).

Plasticity in reproduction can be exacerbated by inter-annual variability in other types of "resources" such as pollen. While no information exists on the mating system of southern California coastal populations, in general, *L. glabrata* subsp. *coulteri* has been categorized as one of the 14 of 17 *Lasthenia* species that is self-incompatible (Ornduff 1966). Several species of insects such as bees, beeflies, flies, and beetles were observed visiting flowers, although what role these species have in effecting pollination of *L. glabrata* subsp. *coulteri* is unknown. Based on the species' presumed status as an entomophilous outcrosser, reproductive yield must depend to some degree on pollination success. As with their host species, pollinators, some of which are believed to nest in marshes or adjacent upland areas, can be affected by climatic variations and watershed disturbances, including flooding (Stephen et al. 1969).

Given the myriad of ecological interactions involved, it is not surprising that the factors governing reproductive potential and success of *L. glabrata* subsp. *coulteri* may prove complex both in terms of time and scale. A number of recent studies have supported the potential for spatial or temporal heterogeneity in resource and pollen limitations (McCall and Primack 1987; Zimmerman and Aide 1989; Campbell and Halama 1993; Lawrence 1993;

Parsons 1994; Parsons and Zedler 1997). Our study supports not only inter-annual heterogeneity in resource limitations, but possibly intra-annual heterogeneity, as well. For example, while reproductive potential and rainfall totals between October–March were similar for the 1996 and 1999 San Dieguito Lagoon populations, seed set was higher in 1999 than in 1996. A series of storms in early April 1999 may have eased resource constraints during the seed set period, allowing the sparse population of small plants to produce comparatively larger numbers of seed. In general, however, the complex hydrology of urbanized watersheds with dams, year-round urban run-off, and mouth closures would seemingly argue against a tight linkage between rainfall patterns and resource inputs and cycling.

CONCLUSIONS

As we originally surmised, the *L. glabrata* subsp. *coulteri* population at San Dieguito Lagoon is not only smaller than the one at San Elijo Lagoon, but, based on trends in seed production, less stable, as well. For the most part, plants at San Dieguito Lagoon were smaller and produced less flowers and capitulescences and seed than those at San Elijo Lagoon. However, the nature of this relationship appears to be temporally variable and highly dependent on climatic conditions such as rainfall totals and distribution. In a year with above-average rainfall, yield of the San Dieguito Lagoon population was similar to and, in some ways, greater than that of the more stable one at San Elijo Lagoon. As rainfall is often linked directly and indirectly to inputs and cycling of resources such as water and nutrients, the strong association found between resources and reproductive potential and, to some extent, reproductive success is certainly not surprising, although the relationship was not always either simple or linear. Too much water actually appeared to decrease survival and reproductive yield of the 1998 San Elijo Lagoon population by inducing "waterlogging." In addition, some nutrients such as inorganic nitrogen and phosphorous may require higher levels of other resources such as soil moisture before exerting a positive effect on growth or reproduction of *L. glabrata* subsp. *coulteri*. When resources are sufficient, seed production appears to be limited by other "resources," the most probable of which is pollen supply.

The importance of the relationship between climatic conditions and population productivity assumes a deeper significance when considering the long-term viability of the small San Dieguito Lagoon population. Obviously, less seed will be produced in years when few plants are present or plant vigor is reduced. Still, even when the San Dieguito Lagoon population was relatively large and produced more seed per plant than the San Elijo Lagoon one, productivity of the San Dieguito Lagoon

population as a whole was still comparatively lower, because of the difference between marshes in population size. To some extent, the impact of consistently producing small numbers of seed could be offset if seed banks are long-lived and/or seed viability and germination rates are high. No research has been specifically conducted on seed bank longevity of *L. glabrata* subsp. *coulteri,* but studies on various *Lasthenia* species have documented long-lived seed banks (10 y; Vivrette 1999) and high germination rates in the field (25 to 69 percent; Thorp 1976) and laboratory (34 to 90 percent; Kingsbury et al. 1976; Callaway et al. 1990; Rajakaruna and Bohm 1999; Michael Wall personal communication, March 1999; Doug Gibson unpublished data). However, there are indications that germination or emergence from the seed bank for some *Lasthenia* species may be tightly regulated by the same climatic conditions (Vivrette 1999) that appear to negatively affect yield of *L. glabrata* subsp. *coulteri,* at least at San Dieguito Lagoon. Some evidence for this could be seen in the low number of plants present at San Dieguito Lagoon in 2000 (six plants; A. Thorpe personal communication), when rainfall during the primary germination period (October—January) totaled only 10.4 percent of average (San Diego NWS-Lindbergh; California Department of Water Resources, California Data Exchange Center). In drought years, then, both recruitment and individual yield could be reduced, thereby further diminishing productivity of the population as a whole.

Poor recruitment and yield in all but above-average rainfall years is of concern for populations in a region such as southern California, where above-average rainfall years are sporadic and often interspersed between lengthy periods of drought or below-average rainfall. In San Diego County, below-average rainfall occurs 60 percent of the time, while above-average rainfall occurs about 40 percent of the time (Elwany et al. 1998). There are suggestions that variability of this already extremely variable climate may be increasing due to global warming. Chronically low numbers of plants in average to below-average rainfall years can increase populations' susceptibility to genetic bottlenecks or extinction due to stochastic or disturbance-related events. Long-term viability of small populations such as San Dieguito Lagoon will probably depend on whether the species can germinate and reproduce successfully under average, as well as above-average, rainfall and climatic conditions. Future monitoring efforts should focus on assessing reproductive potential and success of this population under a variety of climatic and hydrologic conditions, as well as better defining pollinator relationships, breeding system, survivorship, seed bank dynamics, and field germination rates of *L. glabrata* subsp. *coulteri.*

IMPLICATIONS FOR MANAGEMENT AND RESTORATION

The information from this study will provide both preserve and restoration managers with some guidelines for future efforts to enhance or even reintroduce *L. glabrata* subsp. *coulteri* into salt marshes. Based on our results, *L. glabrata* subsp. *coulteri* grows best in marshes with moist, but not waterlogged, soils with low to moderate salinity, high cation exchange capacity, high percentage of organic matter, and moderate concentrations of phosphorous, calcium, and possibly ammonium. To ensure a high potential for project success, managers interested in conducting enhancement or reintroduction projects should carefully evaluate site conditions and hydrologic management regimes. While the goal of restoration and enhancement continues to revolve around creation of self-sustaining ecosystems, the reality is that many of our wetland ecosystems are now highly managed through tide or sluice gates, dikes, culverts, mechanical mouth breaching, and even deliberate floodings to attract waterfowl. If management cannot be avoided, it can perhaps be manipulated to provide benefits to species other than waterfowl. Indeed, the high yield recorded at San Elijo Lagoon in years with below-average rainfall may result in part from artificially elevated soil moisture conditions created by back-up of run-off and creek flows when sluice gates are closed during the winter.

While, as a science, restoration ecology has moved away from a single-species management approach, there is still a strong need for single-species-focused research. Without carefully understanding the biotic and abiotic relationships that drive individual species within an ecosystem, we might be tempted to make gross generalizations about the habitat linkages without ever really grasping the framework of those linkages. For example, what functions of the high marsh are particularly important for *L. glabrata* subsp. *coulteri,* and how do these needs complement or detract from those of other species inhabiting this fragile ecotone, such as *Cordylanthus maritimus* Benth. subsp. *maritimus* or *Panoquina errans* (wandering skipper butterfly)? Directed research on each of these species provides the pieces for the larger ecosystem puzzle. It is up to restoration and preserve managers to put the puzzle together in a manner that will maximize benefits for as many species as possible, as well as the ecosystem as a whole.

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PLEISTOCENE MACROFOSSIL RECORDS OF FOUR-NEEDLED PINYON OR JUNIPER ENCINAL IN THE NORTHERN VIZCAINO DESERT, BAJA CALIFORNIA DEL NORTE

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Abstract

Two late-Pleistocene *Neotoma* (wood rat) middens have been dated by four radiocarbon analyses at 10,000–10,200 and 17,470 radiocarbon years. Both deposits document by numerous macrofossils the abundance of *Juniperus californica* Carrière, but in the older deposit dominance is shared with *Pinus quadrifolia* Parl. Both deposits contain lesser quantities of the principal dominant shrub of the California chaparral, the chamise (*Adenostoma fasciculatum* Hook. & Arn.) together with the shrubby oak, *Quercus turbinella* E. Greene, and other chaparral genera at about 30°N in the northern part of the Vizcaino desert. The existing desert vegetation at both sites is dominated by giant columnar xerophytes and several species of low, desert shrubs, no trace of which has been detected in either of the dated middens. Although abundance of macrofossils of woodland trees with lesser amounts of chaparral shrubs, in conjunction with absence of any species of desert shrub, document a modest displacement of desert vegetation at moderate elevations (550–594 m) in the northernmost Vizcaino desert, this evidence cannot be extrapolated to include the entire peninsula of Baja California. Very substantial biogeographic and ecologically pertinent physiographic evidence suggest a major desert barrier in the central part of the peninsula that also may explain the high degree of endemism in the desert flora.

Resumen

En Desierto Vizcaino, Baja California del Norte, Mexico, en 550–594 m, dos depositos de epoca tardo-Pleistocene con datos 10,000–10,200 y 17,470 anos, documentan con macrofosiles numerosos la presencia de *Pinus quadrifolia* y/o *Juniperus californica,* con arbustos de encinal (*Quercus turbinella, Adenostoma fasciculatum*). Sin embargo, arbustos de desierto moderno ausente en los dos depositos.

Some of the most spectacular desert vegetation in North America occupies a relatively restricted sector of northern Baja California, north of the Vizcaino Plain in the central part of the peninsula. Shreve (1951), who was very familiar with all the North American deserts, referred to it as a desert wonderland (on p. 108). This unique assemblage of bizarre xerophytes of gigantic stature extends from just south of the lofty Sierra San Pedro Martir, east of El Rosario on the Pacific Coast, south to about San Borja, a distance of about 250 km. The most spectacular scenery is more localized, reaching a peak in areas of weathered granitic rocks, such as the extensive tract north of Santa Ines or farther south near Portezuelo.

The unique plant is the cirio tree (*Idria columnaris* Kell.), a remote relative of the common ocotillo (*Fouquieria splendens* Engelm. also present) of the same family, but the cirio attains a height of more than 16 m and has a single main trunk with spongy wood that stores water. It has been likened to an inverted, spiny carrot with innumerable short branches arranged in dense spiral phyllotaxy. Although it resembles a giant columnar cactus, it has ordinary C3 photosynthesis, unlike most cacti which have crassulacean acid metabolism (CAM). The cirio is practically endemic to this sector of Baja California, reaching its southern limit on the high Tres Virgenes volcanoes at over 1600 m, east of San Ignacio. The equally impressive cardon cactus (*Pachycereus pringlei,* (S. Wats.) Britt. & Rose) has about the same northern limit on the Pacific slope, but extends south to the Cape in Baja California del Sur, where it is the ubiquitous dominant giant of desert elevations.

Another pachycaul with a swollen trunk, the elephant tree (*Pachycormus discolor* (Benth.) Coville) is prominent in the cirio area but extends south with the cardon, though not nearly to the Cape. Closer to the cardon in distribution is another distinctive quasi-endemic tree, *Viscainoa geniculata* (Kell.) Greene, which associates with cirio in its more limited range. Sprawling beneath the vertical cardons is another large cactus, but of a horizontal mode of growth, the endemic *Machaerocereus gummosus,* (Engelm.) Britt. & Rose, with a windswept appearance and tart fruits ("pitahaya agria"). The lesser cacti include various species of *Opuntia,* especially chollas (*O. cholla* Weber, *O. molesta* Brandegee). A lesser succulent is the euphorbiaceous *Pedilanthus macrocarpus* Benth. The dominant understory shrubs are mainly dull gray like *Ambrosia chenopodiifolia* (Benth.) Payne, enlivened by weedy patches of *Encelia californica* Nutt. with its masses of sunflowers, and punctuated by the scarlet flowers of *Beloperone* shrubs (seen after the winter rains).

TABLE 1. PLANT COMPOSITION OF *NEOTOMA* MIDDENS FROM THE CIRIO-CARDON DESERT OF BAJA CALIFORNIA DEL NORTE. Locations shown on Fig. 1: site 1 = northwest of Mision San Fernando at ca. 30°N; site 2 = northwest of Rancho Santa Ines at 29°46′N. Relative abundances: +++ = major constituent; ++ = lesser; + = trace.

	SITES: AGES:	San Fernando, at 594 m 10,000–10,200 ± 135 (UCLA: 1365, 1366, 1367)	Santa Ines, at 550 m 17,470 ± 200 (Beta 9372)
MACROFOSSILS			
CONIFERS			
Pinus quadrifolia (intact leaf fascicles)		absent	+++
Juniperus californica (leafy twigs, seeds)		+++	+++
CHAPARRAL			
Adenostoma fasciculatum var. *obtusifolium* (leaves)		++	++
Quercus turbinella (acorns, leaves)		++	++
Prunus lyonii (leaves, endocarps)		+	+
Arctostaphylos glandulosa (nutlets of drupe)		+	
Eriodictyon angustifolium (leaf)			+

It was in this most spectacular part of Baja California that I first sought for evidence of Pleistocene vegetation early in 1968. The *Neotoma* method (Wells 1976) had already proven fruitful in the Mohave, western Sonoran ("Colorado" desert, California), and Chihuahuan deserts (Wells 1966; Wells and Berger 1967). Equipped with a ¾ ton 4 × 4 pickup and camper, my lifetime friend, Jack Yrizarry, and I crawled down the thousand-mile desert track to the Cape. "The Baja Run" was then little more than a very rough, rocky trail with incredibly steep grades in places and was strictly one lane in the best stretches, where a speed of 15 mph might be briefly reached! The average speed with a big, rocking camper was about 5 mph. That there was any "road" at all was due to a sparse procession of big-wheeled trucks driven by native truckers, who provided "servicio particular" to isolated local rancheros.

METHODS AND MATERIALS

The *Neotoma* macrofossil method (first monographed in Wells 1976) is deceptively simple, but requires thorough training in taxonomic and morphological botany and proficiency with existing floras over wide areas of North America. Furthermore, it is essential that proficiency extends to minute details exhibited by numerous tiny macrofossils. Interpretation of the results requires training in ecology of the vegetation of North America and detailed knowledge of its physiography, geology, and climatology.

Skilled sampling of the deposits is even more essential. The key to critical stratigraphic analysis is a focus on friable, macrofossil-rich layers. The friable stratigraphic layers are split off as separate units that disintegrate in the dry state into their constituent macrofossils. Thus, bulk-processing of middens in homogenizing water baths is avoided. Instead, the method of dry-processing provides a copious yield of macrofossils from discrete stratigraphic units that are carefully sorted on a multiple-mesh seive set. The macrofossils are sorted as to species, weighed, and reported as percent biomass, or with simpler assemblages assigned relative abundances. Most species are present as mere traces. There is often an overwhelming dominance of woody plants that fully justifies the vernacular name "wood rat," coined by mammalogists for the genus *Neotoma*. Aliquots of the same friable stratigraphic layers burned for carbon dating are curated separately as vouchers for documentation and further study.

RESULTS

Less than a week of crawling south of Ensenada got us well within the northern part of the great cirio desert, northwest of Mision San Fernando. Exploring all of the rock shelters we could spot with 10× binoculars en route, we finally found an old wood rat (*Neotoma*) midden in a cavelet located in volcanic rocks. The midden was about one meter thick and well within a secure shelter, large and dark enough to harbor a few bats. I knew it was old because it contained none of the desert plants mentioned above, but rather was composed of woodland or chaparral trees and shrubs, predominantly *Juniperus californica,* accompanied by leaves and acorns of a shrubby live-oak (*Quercus turbinella*) and tiny but numerous leaves of chamise (*Adenostoma fasciculatum*), a principal dominant of the California chaparral (Table 1). Also present were a few nutlets of *Arctostaphylos glandulosa* Eastw. More remarkable were the large leaves and endocarps (cherry pits) of *Prunus lyonii* Eastw., the Catalina cherry.

A thorough reconnaisance of the area showed a desert vegetation characterized by dominance of all of the giant columnar xerophytes and a profusion of lesser cacti and Agavaceae, notably *Agave shawii* Engelm., *A. deserti* Engelm., and *Yucca whipplei* Torrey. There were no chaparral shrubs except for one individual of the xerophytic monotype, *Xylococcus*. A fly in the ointment was the presence of a few, live *Ju-*

niperus californica Carrière about 200 m from the midden site at an elevation of 610 m (2000 ft). This somewhat vitiated the significance of the juniper record, but the chaparral sclerophylls justified the three radiocarbon dates kindly provided by Rainer Berger: 10,000 to 10,200 radiocarbon years before present from top to bottom of the midden. This was cetainly not a pleniglacial date, but rather late-glacial to Holocene transition (Table 1).

Proceeding slowly south for another few days, we entered the extensive granitic area north of Santa Ines, where we explored many *Neotoma* middens in cavities within the small exfoliation domes of the granitoid rocks. Unfortunately, all we saw were records of desert plants. This set a pattern of more desert records all the way to La Paz. Needless to say, I was discouraged with the prospects, but later switched to mainland Mexico, where I have more unpublished records. Still later, I decided to concentrate on the Great Basin (Wells 1983).

Shortly after the 1983 paper appeared, William H. Clark of Albertson College, Caldwell, Idaho, kindly sent me samples of an obviously ancient wood rat midden from the Santa Ines granitic area. It contained *Pinus quadrifolia,* a four-needled pinyon pine species previously unrecorded in the *Neotoma* fossil record anywhere, so I had the stratum dated: 17,470 ± 200 radiocarbon years before present (Beta 9322). In 1988, I responded to Bill's generous invitation to visit the site to collect more material. Instead of a week's drive below Tijuana, I made it in the afternoon of the same day, blacktop all the way! Additional material from the dated sector of the midden provided much more *Pinus quadrifolia* and *Juniperus californica* and a similar assemblage of chaparral sclerophylls previously recorded in the 10,000 yr old midden, plus *Eriodictyon angustifolium* Nutt. Consistently absent from both the 10,000 and 17,400 y-old deposits were any xerophytes of the existing desert vegetation (Table 1).

The combination of chaparral shrubs, junipers, and pinyons was called *encinal* by Forrest Shreve, using a Spanish word for an oak community. The west slope of the Sierra San Pedro Martir at middle elevations has chaparral, partly dominated by *Quercus turbinella* and *Adenostoma,* associated with *Pinus quadrifolia* and *Juniperus californica* but minus any desert xerophytes, aside from the chaparral *Yucca, Y. whipplei.* Thus, the encinal recorded in late-glacial and pleniglacial middens in what is now cirio desert has a nearly exact analog in the San Pedro Martir mountains to the north.

DISCUSSION

The contrast between the spectacular modern desert vegetation dominated by giant xerophytes like cirios and cardons at both *Neotoma* sites and the midden macrofossil evidence for a Pleistocene encinal, lacking desert xerophytes, staggers the imagination (Table 1). The recorded displacement was complete at this latitude, ca. 30°N.

Pinus quadrifolia, the four-needled pinyon, is one of the more mesophytic pinyon pines. At present it is restricted to moderately high elevations (ca. 1100 to 2100 m, or 3500 to 7000 ft), mainly on the western or Pacific slopes of the Peninsular Range as far south as the San Pedro Martir. In contrast, the one-needled *P. californiarum* D.K. Bailey (1987) occurs on the rain-shadowed eastern slope of the Peninsular Range (Bailey, personal communication 1975–1990; Wells 1995). Where the two distinct species occur on the same mountain, as on Mt. San Jacinto, California, *P. quadrifolia* forms a zone well above *P. californiarum.* The latter, one-needled, pinyon alone has a far southern disjunction on Cerro San Luis (to 1550 m) in the Sierra de Calamajue at about 29°N, an isolated peak not far north of the high San Borja Mountains (to 1700 m +), where no pinyon pines have ever been recorded (Fig. 1). The nominate subspecies of *Pinus californiarum* also extends disjunctly far to the north of *P. quadrifolia* on low, isolated mountains in arid parts of the Mohave Desert, e.g., the Coxcombs, Eagle, Old Woman, and northeast in the Providence; it dominates the pinyon-juniper zone in all of these ranges (Wells 1995).

From the distribution maps of Critchfield and Little (1966), one would have hypothesized *P. californiarum* (then under the Great Basin species *P. monophylla* Torrey & Frémont) to have extended farther south on the peninsula than *P. quadrifolia* during the Ice Ages, because they show the southerly outlier of the former on Cerro San Luis. This may well have been true on the east or Gulf of California slope, where we have no *Neotoma* records. The macrofossil record of *P. quadrifolia* we do have is from the Pacific side of the peninsular divide in the cirio zone at the substantial elevation of 550 m (1800 ft), less than 500 m below its modern lower limit (Wells 1986).

The assemblages of evergreen sclerophylls (*Adenostoma fasciculatum,* or chamise, a principal dominant of California chaparral, *Prunus lyonii, Arctostaphylos glandulosa* or Eastwood manzanita, etc.) are consonant with the presence of *Juniperus californica* or *Pinus quadrifolia* in the same strata of the *Neotoma* middens. Today, the juniper and four-needled pinyon both associate with a broad zone of chaparral below montane forest of *Pinus jeffreyi* Grev. & Balf. that is mainly above 2500 m; the chaparral belt (largely dominated above by *Arctostaphylos peninsularis* Wells) extends down to <1000 m.

Chaparral extends southward from California in the Peninsular Range to Cerro Matomi (to 1370 m), the southern extremity of the San Pedro Martir. Aside from small populations of manzanitas (*A. peninsularis*) on isolated peaks: Cerro San Juan de Dios (to 1300 m at 30°N) and Cerro San Luis (1550 m: the southern limit of *Pinus californiarum* at 29°19'N) there is a major disjunction of chaparral species to the high San Borja Mountains (to 1700
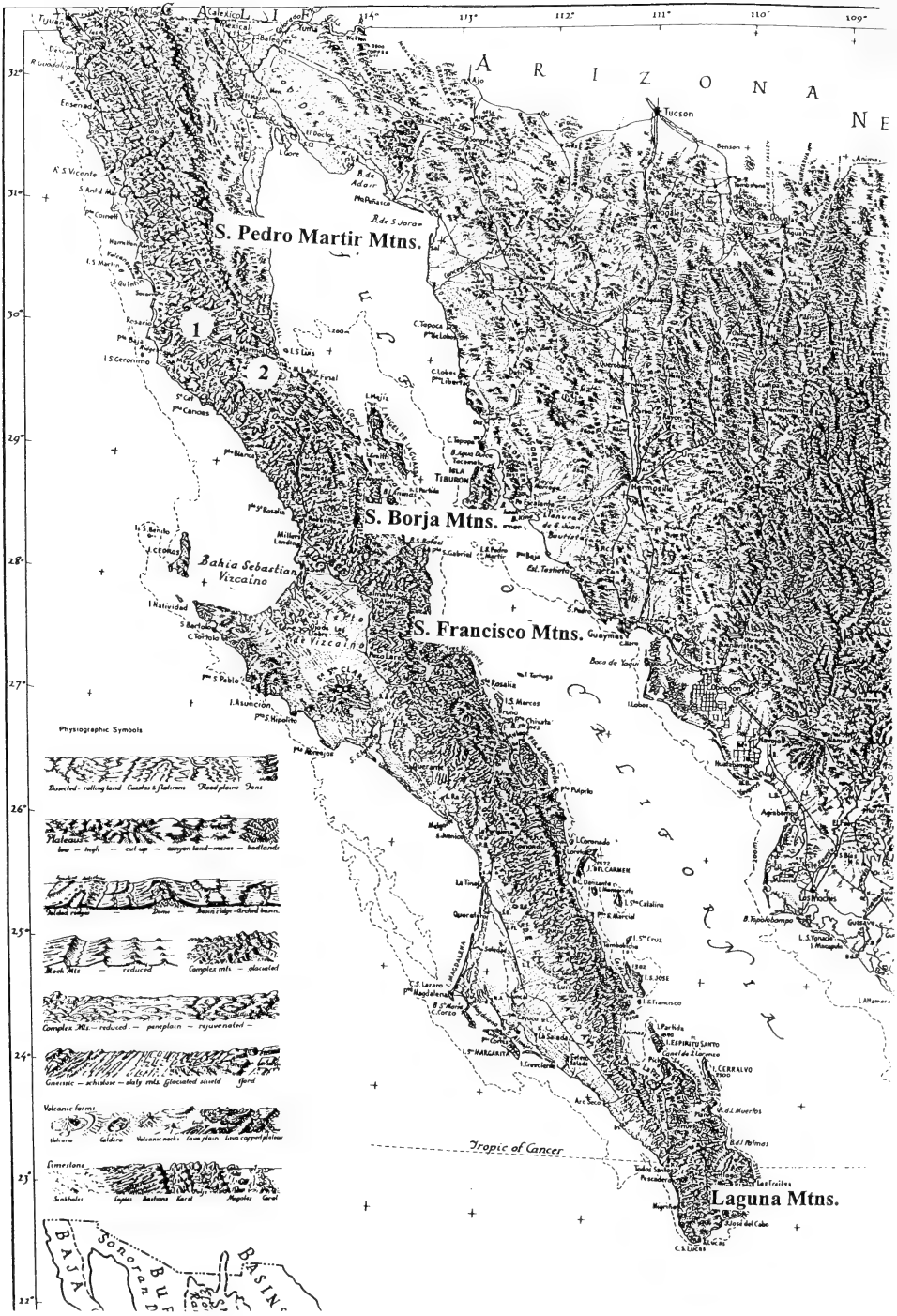
Fig. 1. Map of Baja California, showing principal mountains mentioned in text and numbered wood rat (*Neotoma*) midden sites of Pleistocene age in white circles: 1 = northwest of Mision San Fernando, 30°N, at 594 m (1950 ft). 2 = northwest of Rancho Santa Ines, 29°46′N, at 550 m (1800 ft).

m) rising above the Gulf of California at 28°47′N (Fig. 1). The San Borjas are the southern limit of *Juniperus californica* and *Arctostaphylos peninsularis,* but lack pinyon pines (Reid Moran, personal communication 1969; Wells 1972). Still farther

south at 27°30′N there is a southern outpost of chaparral on the lofty Tres Virgenes volcanoes (to 2000 m) above Santa Rosalia on the Gulf; the Tres Virgenes are also a southern outpost for cirio trees.

Possibly the most unexpected macrofossil occur-

rence in the northern cirio desert at both *Neotoma* sites (Table 1) is the Catalina cherry tree (*Prunus lyonii*). This large-leaved cherry occurs in California on the larger Channel Islands, but not on the mainland. In Baja California, however, this ever-green cherry has widely disjunct stations in deep canyons of the isolated and inaccessible Sierra de San Francisco (or Francisquito) of northern Baja California del Sur at ca. 27°30′N (Fig. 1). The two Pleistocene records of *Prunus lyonii* in the northern part of the cirio zone suggest (but do not prove) a former continuity of range.

A major biogeographic anomaly that might shed light on the Pleistocene location of the Sonoran Desert with its rich array of endemic plants (about 30% of the 2500+ species are endemic: cf. Wells 1970), is posed by the distribution of pinyon pines (cf. Wells 1986). As discussed above, *Pinus quadrifolia* is presently restricted to the Sierra San Pedro Martir south to about 30°20′N, and the *Neotoma* record at Santa Ines extends that to 29°46′N, a scant 80 km farther south. The one-needled *Pinus californiarum* has an isolated southern outpost on Cerro San Luis (to 1550 m) at 29°19′N. Neither of these pinyon pines is known from the higher Sierra San Borja (to 1700 m +), where *Juniperus californica* reaches its southern limit. None of these three conifers occurs in Baja California del Sur, the southern half of the peninsula, which has suitably high mountains such as Tres Virgenes (to 2000 m), Sierra de Santa Lucia (to 2000 m), Sierra de la Giganta (to 1770 m), and Sierra de la Victoria (to 2070 m) = Laguna Mountains (Fig. 1). Instead, the Laguna Mountains support an extensive zone of the three-needled Mexican pinyon, *Pinus cembroides* Zucc. (subsp. *Lagunae* Bailey), which has very distinctive pink "endosperm" (gametophytic tissue). In all other species of pinyon pines the food reserves of the seed are white. *Pinus cembroides* has a very wide distribution on the mainland of Mexico. There are also some live-oaks in the Lagunas identical to mainland species (*Quercus reticulata* H. & B., *Q. tuberculata* Liebmann).

Other broad sclerophylls in the isolated Lagunas include the toyon, *Heteromeles arbutifolia* (Lindley) Roemer, *Arbutus peninsularis* Rose & Goldman, and *Garrya salicifolia* Eastw. Most remarkably, no taxa of *Arctostaphylos, Ceanothus,* or *Adenostoma* are known from any mountains of Baja California del Sur (S. de la Giganta, S. de Laguna). Absence of these three most characteristic genera of the California chaparral, including the two most speciose genera, *Arctostaphylos* and *Ceanothus,* is strong evidence of a major isolating barrier in the central sector of the peninsula. The southernmost known occurrence of *Arctostaphylos peninsularis* is in the high Sierra de San Borja at 28°45′N (Wells 2000).

The isolated Sierra de la Laguna pinyon-oak woodland is mainly above tropical deciduous forest, which occupies the lower slopes and surrounding foothills of the Lagunas that are on the Tropic of Cancer (23 ½°N). The absence of *Juniperus californica* or either of the two northern pinyons may mean that these conifers never migrated this far south. Almost certainly, had *Juniperus californica* colonized any of the high mountains of Baja California del Sur, possibly even the summer-rainy Lagunas, it may have survived to the present, inasmuch as its niche is vacant, there being no other species of *Juniperus* in Baja California.

Although the *Neotoma* macrofossil evidence from the northern cirio zone documents a modest displacement of desert vegetation by a mesophytic pinyon pine and evergreen chaparral, there is as yet no evidence as to how far south this Pleistocene climatic effect extended. Even if all the elevated areas north of the Vizcaino plain in the central sector of Baja California were affected, there would be ample room for desert vegetation farther south (Fig. 1). The peninsula is immensely long, extending far into subtropical latitudes. The apparent failure of even the relatively xerophytic *Juniperus californica* to colonize any of the mountains of the southern half of Baja California (it stopped far short in the San Borjas at 28°45′N) suggests a major desert barrier in the central sector of the peninsula, where temperature-sensitive giant cacti, and quasi-endemics like *Idria* (cirio), *Pachycormus, Viscainoa* and others may have survived the long Pleistocene periods of climatic displacement unscathed.

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SEED BANKS OF LONG-UNBURNED STANDS OF MARITIME CHAPARRAL: COMPOSITION, GERMINATION BEHAVIOR, AND SURVIVAL WITH FIRE

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ABSTRACT

Seed germination requirements in the California chaparral have been described mainly from freshly collected seed. However, uncertainties remain because the behavior of seeds in the soil can differ. I studied germination of the seed bank in long-unburned stands of maritime chaparral in central coastal California. I quantified seedlings emerging from soil samples provided with appropriate temperature and moisture conditions following 1) no other treatment, 2) a heat treatment to optimize germination of heat-stimulated species, 3) the same heat with the addition of charred wood, and 4) the burning of chaparral stands prior to collection of samples. I compared germination in these treatments with seedling emergence in the field following fire. I also collected and divided samples into 0–2.5 and 2.5–7.5 cm depth fractions to evaluate abundance of seed at the surface and depth before and after fire.

Seed of one annual had reduced germination following the heat treatment. Seeds of all other species common enough to evaluate statistically were heat tolerant. However, because seeds were found to be mostly near the surface, there was considerable mortality with fire. Moreover, seedling populations in the field only accounted for a fraction of the seed bank that survived fire, and seventeen species that germinated in samples did not germinate and/or emerge in the field. Most species' germination and emergence was influenced in some way by heat and/or charate. Germination of two *Ceanothus* was dependent on heat. *Adenostoma fasciculatum* Hook. & Arn., *Arctostaphylos purissima* P. Wells, and two annuals had germination that was enhanced by heat and enhanced further when charate was added. Despite the importance of fire effects, there were no short-lived species having entirely fire-dependent germination. Germination and/or emergence of 3 species was negatively affected by charate. These germinated sparingly or not at all after fire.

One of the most prominent evolutionary specializations to fire exists in the germination ecology of seeds from plants found in Mediterranean shrublands, particularly those of Australia, South Africa, and California (Bond and Van Wilgen 1996). This subject has received considerable attention (Review by Keeley 1991), revealing a fascinating complexity of features that insure germination will coincide with the anomalously favorable conditions for seedling establishment that exist after fire. There are physical features such as bradyspory (or serotiny) where seeds stored in fruits and cones are released when heated by fire (Whelan 1995), and impervious seed coats that open with the heat of fire (Sweeney 1956; Quick and Quick 1961; Auld and O'Connell 1991). Physiologically dormant seed may be induced to grow following fire by chemicals washed from charred wood (Wicklow 1977; Keeley 1984, 1987; Keeley et al. 1985; Keeley and Pizzorno 1986), water soluble nitrogenous compounds (Thanos and Rundel 1996) and smoke (Keith 1997; Keeley and Fotheringham 1997, 1998). For each fire-related germination cue, there are multiple dormancy-releasing mechanisms that have evolved convergently among disparate floras (Baskin and Baskin 1998). In chaparral, germination without fire may also be inhibited by allelopathic chemicals washed from foliage or litter (Muller et al. 1968; McPherson and Muller 1969), and/or phytotoxins produced by soil microbes (Kaminsky 1981). Fire eliminates these compounds.

Seeds of chaparral plants range from readily germinable at the time of dispersal (non-refractory) to deeply dormant (refractory) as a result of multiple barriers to germination (Keeley and Fotheringham 1998). Some species produce a portion of seed that is refractory and a portion that is not (Emery 1988; Parker and Kelly 1989). Generalizations about the type(s) of dormancy species exhibit derive mainly from tests on freshly collected and stored seed. Germination of seeds residing in the soil may differ significantly, as has been documented for *Adenostoma fasciculatum* Hook. & Arn. and *Arctostaphylos canescens* Eastw. among others (Stone and Juhren 1951; Parker 1987; Keeley and Fotheringham 1998). Seeds exposed to allelopathic chemicals and phytotoxins found in chaparral soils may exhibit enforced dormancy (Muller et al. 1968; McPherson and Muller 1969; Keeley 1991). Therefore, it is imperative to study the soil seed bank to understand how chaparral germination is controlled in nature.

The potential for germination in the chaparral seed bank without fire is thought to be low for most species because seedlings are rarely apparent under

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the shrub canopy. However, Christensen and Muller (1975), Tyler (1995), and Swank and Oechel (1991) reported considerable seedling growth under *Adenostoma* in plots protected from herbivory, suggesting more germination can occur without fire than is evident. In addition, Zammit and Zedler (1988, 1994) and Holl et al. (2000) found that many species germinated readily from chaparral soil seed bank samples. To test how much germination can occur in species' seed banks without fire and how much requires heat and/or chemicals produced by fire, I compared emergence from controls and uniform fire treatments that are known to maximize germination of refractory seed without inducing mortality. I then analyzed how much of the *in situ* seed bank was eliminated above and below 2.5 cm in the soil by fire in the chaparral stands. Finally, I enumerated seedling emergence in the field to compare germination in nature vs. in collected samples.

The chaparral I studied is geographically-isolated and its environment differs in many respects from that found in the Transverse and Peninsular ranges inland. With Santa Ana winds absent, and a lower frequency of ignitions, coastal environments have likely supported less frequent and dynamic fire, at least prior to human dominance of the fire regime (Odion et al. 1992; Odion et al. 1993). The average lifespans of the *Ceanothus* spp. in maritime chaparral are particularly short (Davis et al. 1988) compared to those inland (Keeley 1975, 1992). Death of the non-sprouters opens space for recruitment by numerous herbs and subshrubs (Odion and Davis 2000). These and other factors such as soil and climate may help explain differences in post-fire regeneration in maritime vs. nearby inland chaparral reported by Tyler (1995); they may also have contributed to evolutionary divergence in maritime chaparral taxa that has produced endemic *Arctostaphylos* and *Ceanothus* (Griffin 1978). I have evaluated my germination data for any evidence that the environment and insular nature of the study area manifested variation in germination ecology.

Study Area

Samples were collected from *Adenostoma fasciculatum* (hereafter *Adenostoma*) chaparral located near sea-level, within Vandenberg Air Force Base in central, coastal California as described in D'Antonio et al. (1993), and Odion and Davis (2000). Substratum here is Pleistocene eolian sand (Dibblee 1950). Climate in the area is strongly influenced by the prevailing onshore winds and cool ocean, and the temperature regime is mild, especially for a chaparral environment. Maritime chaparral of the area has been described in detail by Davis et al. (1988). The average annual precipitation is 35.3 cm. I counted annual rings from the obligate seeders, *Arctostaphylos purissima* P. Wells, and *Ceanothus cuneatus* (Hook.) Nutt. var. *fascicularis* (McMinn) Hoover (Keeley 1993) to establish that the chaparral had not burned for 75–80 y at the site where more intensive sampling was undertaken (site 1). Samples were also collected from a second, nearby site which had not previously burned for about 50 y. Both sites were dominated by *Adenostoma*.

Methods

Transects consisting of 47 contiguous 1 m² plots were established in dense chaparral dominated by *Adenostoma*. Nine 5 cm diam, 7.5 cm deep cores of soil were obtained per plot at site 1 in the fall of 1988. Five cores were collected in fall, 1989 at site 2. Chaparral at both sites was burned soon thereafter, with low fuel moisture contributing to relatively intense fires (Odion and Davis 2000). I collected 5 cores per plot the day after each fire. Seed bank cores for each plot were composited, and 350 cc subsamples were removed from each homogenized sample.

Pre-burn samples from site 1 were given three treatments: 1) heat, 2) heat and charate (charred, pencil-sized *Adenostoma* stems collected after the fire and ground up) and 3) control (no heat or charate). Only the second of these treatments was used on pre-burn samples from site 2. Samples to be heated were spread to a depth of 2–3 mm on aluminum cooking trays. Based on studies by Wright (1931), Sampson (1944), Sweeney (1956), Keeley and co-workers (several publications, see Keeley (1991), heating at 100°C for ~5 min typically produces the greatest germination response among fire-recruiters, and is well within their heat tolerance. Given the slight insulation the soil would provide, I decided to use a 7 min duration. Heat-induced seed mortality is controlled predominantly by maximum temperature, as opposed to duration (Borchert and Odion 1995), so it is unlikely that this change effected mortality. Heating was done in a forced-air oven.

The subsamples were spread on sterile sand in 20 cm plastic pots. The amount of charate added was 2 rounded tablespoons (21.3 ± 0.94 g, n = 11).

The pots were covered with clear plastic, protected from herbivory, and kept moist out-of-doors under 50 percent shade cloth at Cal-Orchid Nursery in Santa Barbara, where temperature fluctuations were analogous to the field. Potting was complete in late November, at which time all samples were given their first watering. All the samples were exposed to outdoor temperatures from the time of collection through the subsequent growing season to provide natural temperature stratification.

Seed bank sampling was also undertaken at randomly located ~1.5 m diam canopy gap areas adjacent to the site 1 transect. I took samples from the center of the gap as well as the edge and understory of the adjacent *Adenostoma* canopy. These cores were separated into 0–2.5 cm and 2.5–7.5 cm

depth fractions and given the heat and charate treatment. Due to smaller amounts available, 175 cc subsamples were spread over sand in 16 cm diam plastic pots placed with the others.

All germinants were identified and removed from pots through the growing season. Nomenclature follows Hickman (1993). Specimens whose identity was uncertain were grown until it was determined. Five of the pre-burn samples treated to heat and charate were removed from pots after emergence stopped. I repotted these the following autumn. No further germination occurred in these.

RESULTS

General patterns. Seed from 72 species germinated and emerged from samples collected along transects (Table 1). More than half (48) were annuals. Site 2 had greater diversity (60 vs. 48 species). Many of the same species emerged abundantly from samples from both sites (e.g., *Adenostoma, Helianthemum scoparium* Nutt., *Crassula connata* (Ruíz Lopez & Pavón) A. Berger, *Centaurium davyi* (Jepson) Abrams, and *Navarretia atractyloides* (Benth) Hook & Arn.). Despite this, there were only 33 species in common. In addition, two subshrubs, *Mimulus aurantiacus* Curtis and *Lotus scoparius* (Nutt.) Ottley, were abundant in site 2 samples and absent in those from site 1. Several annuals were common in samples from one site but not the other. Nine species were non-native. All 9 are widespread weeds.

Post-burn samples contained 44 species (1 non-native) and substantially reduced numbers of germinants. The reduction varied with species depending on the proportion of seed present at depth, as described below. Reduced germination was also strongly correlated with the amount of soil heating that occurred where samples were located (Odion and Davis 2000). Thus, the number of post-burn germinants was much greater in samples from gaps vs. under the shrub canopy. Horizontal patterns of seed abundance are analyzed in Odion and Davis (2000).

There were 20 and 31 species that germinated in the field respectively at the two sites (Table 1). Twelve were at both. Four species germinated in the field plots but not seed bank samples. There was only one individual of each. Seventeen species germinated in samples but did not germinate and/or emerge in the field, including species whose seed was among the most abundant (e.g., *Centaurium davyi, Mimulus floribundus* Lindley). Another, *Crassula connata,* was virtually absent in the field in the burn areas, although it was common in adjacent unburned chaparral. Field populations for most species were much smaller than post-burn seed bank populations—between ~5 and 14 times smaller for shrubs, and generally even smaller for other species.

Germination treatments. Only two species, both

perennial *Gnaphaliums,* had germination that was not affected by the heat treatment (Table 1). One of these, *G. microcephalum* Nutt. was significantly negatively affected by charate. Among heat-affected species, the two obligate-seeding species of *Ceanothus,* the subshrub *Helianthemum scoparium,* and the annual *Trifolium microcephalum* Pursh had significantly greater germination with heat alone, while the opposite occurred for the annual *Calandrinia ciliata* (Ruíz Lopez & Pavón) DC. (Table 1). Other important species that had a positive response to heat were also affected by charate. *Adenostoma, Arctostaphylos purissima,* and *Lotus strigosus* had significantly greater germination with heat and charate compared to heat alone.

Germination of *Centaurium davyii* and *Crassula connata* with heat and charate was not only significantly lower than with heat alone, but also lower than with no treatment. *Crassula* was rare in the burn areas, and *Centaurium* did not occur there until the third year after fire. Both species were fairly common in the surrounding unburned chaparral. *Mimulus floribundus* had much lower germination with heat and charate than with heat alone, but heat and charate germinants outnumbered those in control samples (P > 0.05, NS). This species, though abundant in several samples, was absent from most. It was never observed in the field, including in unburned chaparral. It is typically found in seasonal wetlands like two other species that were found in samples, but not in the field, *Crassula aquatica* (L.) Schönl. and *Centunculus minimus* L.

With a relatively high proportion of seed at depth (76 percent below 2.5 cm in gap, edge, and understory samples combined, Table 2), *Arctostaphylos purissima* had better survival (post-burn/pre-burn = 17 percent) than *Adenostoma* (site 1 = 2 percent, site 3 = 3 percent) which only had 22 percent of its seed below 2.5 cm. These survival percentages are from transect samples. The 2.5–7.5 cm depth samples had relatively little emergence of species with charate-enhanced germination. Seeds of other shrubs were not abundant enough to evaluate depth distribution. The high survival of *Ceanothus cuneatus* at site 2 (33 percent) as well as results from a fuel translocation experiment (Odion and Davis 2000) suggest this obligate-seeder had a high proportion of seed at depth.

Helianthemum scoparium was particularly abundant and not affected by charate, so the effect of the depth distribution of its seed is relatively clear. The subshrub had 53 and 75 percent of its seed bank below 2.5 cm in gap and understory samples respectively. Despite the greater proportion of seed at depth at understory plots, survival was similar there (22 percent) compared to gaps (24 percent). Survival along the site 1 transect was 9 percent (post-burn/pre-burn heat). After fire, 94 percent of *Helianthemum scoparium* seeds were below 2.5 cm in the soil in understory plots, only half were at depth in gap plots.

TABLE 1. Number of Germinants, Expressed as Density per m², Emerging From 47 Seed Bank Samples, Including All Three Pre-burn Treatments (First Three Columns). + indicates a significant positive heat effect, ++ indicates a significant positive charate effect, - indicates negative effect (P < .05, Kruskal-Wallis rank sum test). Emergence from post-burn samples and in the field the first year after fire are shown in columns 4 and 5.

	Site 1					Site 2		
	Control	Heat	Heat and charate	Post-burn	Field	Heat and charate	Post-burn	Field
SHRUBS								
Artemisia californica	0	0	0	0	0	259.6	4.4	.04
Adenostoma fasciculatum	140.8	246.4+	738.5++	17.6	2.1	633.6	17.6	0.2
Arctostaphylos purissima	30.8	180.4+	290.4++	48.4	3.3	0	4.4	0
Baccharis pilularis	13.2	8.8	8.8	0	0.1	44.0	0	0
Ceanothus cuneatus	0	35.2+	30.8	0	1.6	145.2	48.4	10.1
Ceanothus impressus	0	39.6+	57.2	13.2	0.8	4.4	4.4	.02
Ericameria ericoides	22	4.4	0	0	0	0	0	0
Ribes malvaceum	0	0	0	0	0	0	0	.02
Salix lasiolepis	0	0	0	0	0	13.2	22.0	0
Salvia mellifera	0	0	0	0	0	74.8	4.4	66.0
SUBSHRUBS								
Carpobrotus edulis	17.6	35.2	8.8	0	0.1	0	0	0
Eriophyllum confertiflorum	0	0	0	0	0	88.0	0	.06
Helianthemum scoparium	114.4	1689.6+	1346.4	118.8	6.0	6859.6	1456.4	45.0
Horkelia cuneata	0	4.4	0	0	0	8.8	13.2	26.4
Lotus scoparius	0	0	0	0	0	382.8	57.2	3.7
Mimulus aurantiacus	0	0	0	0	0	875.6	30.8	0
Solanum douglasii	0	0	0	0	0	8.8	0	.02
Solanum xanti	0	0	0	0	0	4.4	0	.02
PERENNIAL HERBS								
Carex globosa	4.4	26.4	8.8	4.4	0.1	4.4	0	74.8
Gnaphalium canescens	4.4	13.2	0	0	0	0	0	0
Gnaphalium microcephalum	118.8	198.0	35.2-	0	0	74.8	4.4	0
Gnaphalium ramosissimum	127.6	136.4	105.6	22	0	1258.4	52.8	.02
Melica imperfecta	0	0	0	0	0	4.4	0	0
Mimulus floribundus	118.8	743.6	250.8	0	0	0	44.4	0
Nassella lepida	4.4	22	0	4.4	0	0	0	0
ANNUALS								
Anagalis arvensis	0	0	0	0	0	83.6	4.4	.15
Anthemis cotula	0	0	4.4	0	0	0	0	0
Aphanes occidentalis	0	0	0	0	0	13.2	0	0
Apiastrum angustifolium	8.8	79.2+	57.2	0	1.2	39.6	0	3.4
Calandrinia ciliata	110	39.6-	26.4	0	0.1	57.2	0	0
Calyptridium monandrum	4.4	8.8	0	0	0.1	127.6	17.6	.02
Camissonia micrantha	0	0	0	0	0	105.6	22.0	.04
Centaurium davyi	567.6	1355.2+	365.2-	52.8	0	3049.2	444.4	0
Centunculus minimus	22	167.2+	17.6	0	0	0	0	0
Chorizanthe diffusa/angustifolia	30.8	61.6	30.8	8.8	0.02	22.0	4.4	.15
Conyza canadensis	0	70.4	8.8	8.8	0	0	0	0
Crassula aquatica	0	4.4	0	0	0	0	0	0

TABLE 1. CONTINUED.

	Site 1					Site 2		
	Control	Heat	Heat and charate	Post-burn	Field	Heat and charate	Post-burn	Field
Crassula connata	2094.4	3159.2$^+$	859.8$^-$	228.8	0.2	981.2	347.6	0
Cryptantha clevelandii	0	0	8.8	0	0	114.4	0	0
Cryptantha micromeres	0	0	0	0	0	44.4	4.4	.02
Daucus pusillus	4.4	57.2	17.6	0	0	572.0	127.6	1.5
Epilobium adenocaulon	0	0	0	0	0	4.4	0	0
Eucrypta chrysanthemifolia	0	0	0	0	0	17.6	0	.09
Filago arizonica	8.8	4.4	4.4	0	0	17.6	0	0
Filago californica	8.8	4.4	0	0	0	61.6	8.8	0
Filago gallica	26.4	52.8	26.4	0	0.1	26.4	0	0
Gastridium ventricosum	4.4	0	0	0	0	0	4.4	0
Gnaphalium purpureum	114.4	325.6$^+$	453.2^{++}	0	0	79.2	0	0
Guilleria lasiophyllum	0	0	0	0	0	4.4	0	0
Hypochaeris glabrata	8.8	8.8	0	0	0	13.2	4.4	.02
Juncus bufonius	13.2	61.6$^+$	8.8	0	0	13.4	17.6	0
Juncus sphaerocarpus	8.8	17.6	4.4	4.4	0	0	0	0
Linaria canadensis	48.4	57.2	17.6	0	0.1	250.8	52.8	.06
Lotus hamatus	8.8	30.8$^+$	79.2	13.2	0	8.8	13.4	0
Lotus salsuginosus	4.4	158.4$^+$	39.6$^-$	17.6	2.5	0	0	0
Lotus strigosus	17.6	343.2$^+$	457.6^{++}	26.4	1.3	167.2	26.4	3.7
Melilotus indicus	0	0	0	0	0	0	0	.02
Microseris lindleyi	0	4.4	0	0	0	0	0	0
Navarretia atractyloides	352	585.2$^+$	734.8	180.4	5.2	721.6	79.2	.6
Pectocarya penicillata	0	0	0	0	0	57.2	8.8	0
Polycarpon depressum	0	0	0	0	0	57.2	8.8	.02
Polypogon monspeliensis	4.4	0	0	0	0	0	0	0
Psilocarphus tenellus	0	0	0	0	0	4.4	0	0
Pterostegia drymarioides	0	0	4.4	0	0	57.2	0	.02
Sagina decumbens	0	0	0	0	0	0	0	0
Senecio californica	0	0	0	0	0	4.4	0	0
Silene gallica	0	0	0	0	0	4.4	0	0
Silene multinervia	4.4	0	0	0	0.1	0	0	0
Spergularia marina	0	0	0	0	0.1	0	0	0
Stylocline gnaphalioides	13.2	0	0	0	0	0	0	0
Trifolium microcephalum	4.4	167.2$^+$	110	0	0	8.8	12.2	0
Triodanis biflora	0	0	0	0	0	0	0	0
Vulpia microstachys	0	8.8	4.4	8.8	0.1	44.4	0	0
Vulpia octoflora	4.4	74.8$^+$	74.8	8.8	0.1	492.8	101.2	.5
Unidentified grass	0	0	0	0	0	0	0	.02

TABLE 2.　NUMBERS OF GERMINANTS, EXPRESSED AS AVERAGE NUMBER PER M², FROM 0–2.5 CM AND 2.5–7.5 CM DEPTH FRACTIONS BEFORE AND AFTER FIRE, AND IN THE FIELD FROM THE SAME PLOTS IN WHICH THE SEPARATE DEPTH SAMPLES WERE TAKEN. Values are the averages from 30 samples expressed as the density of seed per m². Pre-burn samples were treated with heat and charate.

	pre-burn		post-burn		field
	0–2.5	2.5–7.5	0–2.5	2.5–7.5	
SHRUBS					
Adenostoma fasciculatum	240.1	52.92	53.9	8.8	5.4
Arctostaphylos purissima	44.1	141.1	36.8	26.5	10.6
SUBSHRUBS					
Helianthemum scoparium	411.6	582.6	88.2	145.6	47.0
PERENNIAL HERBS					
Mimulus floribundus	1519.0	538.0	39.2	26.5	0
ANNUAL HERBS					
Apiastrum angustifolium	245.0	26.5	0	17.6	0.8
Centaurium davyi	1396.5	608.6	558.6	185.2	0
Crassula connata	6056.4	1525.9	1166.2	493.9	1.6
Cryptantha clevelandii	78.4	17.6	0	0	0.1
Lotus strigosus	83.3	88.2	19.6	79.4	11.0
Navarettia atractyloides	3013.5	299.9	274.4	61.7	29.7

Survival percentages of the seed bank for species whose germination was negatively affected by charate are equivocal because post-burn samples presumably contained the inhibitors(s). Among the remaining annuals, high mortality was common. In fact, *Apiastrum angustifolium* Nutt. though fairly common in pre-burn samples, was not detected in post-burn transect samples, and was rare in the field. Seed of this diminutive plant was predominantly near the surface (Table 2). The second most abundant species in the field after fire was the annual *Navarretia atractyloides*. Combining data from gap and understory plots in Table 2, while better illustrating survival at depth, obscured other patterns. Where seed of this species was concentrated, in canopy gap areas, only 6 percent of its seed was below 2.5 cm in the soil, explaining why only 10 percent survived there despite relatively low soil heating with fire. Conversely, in the understory, 16 percent of seed was in the deeper fraction, explaining the relatively high survival (22 percent) along the site 1 transect (predominantly understory). Seed of *Lotus strigosus* (Nutt.) E. Greene was equally abundant in deep and shallow samples overall (Table 2). Survival in surface samples was a relatively high 24 percent, and at depth 90 percent.

DISCUSSION

My procedures indicated that seed mortality with fire was substantial, and greater in the older stand. Previous studies have also found that a significant number of seeds do not survive fire in chaparral (Keeley 1977; Davey 1982; Bullock 1982; Zammit and Zedler 1988; Davis et al. 1989). For species to ensure successful recruitment after fire, their seeds must accumulate at depths in the soil where they will be safe. There must be strong resistance to ger-

mination in the absence of fire for this to occur. Consistent with this, I found that most of the seed bank for many species needed fire to germinate (Table 1). Two shrubs, both species of *Ceanothus,* had germination that was entirely fire-dependent. However, I also found that a small but distinct portion of the seed bank for all other fire-recruiters germinated with simply moisture and natural temperature fluctuations. In addition, there were no short-lived species detected that had entirely fire-dependent germination (*i.e.,* there were no specialized fire annuals), which is not typical for chaparral. Seedlings of these are usually found only the first year after fire (Keeley et al. 1981). Short-lived species in my study all produced seedlings after the first post-fire growing season (Odion 1995, unpublished data). Thus, fire-recruiters in this study, other than *Ceanothus,* produce seed that is both refractory and not. Based on my germination results and those by Davis et al. (1989) and Holl et al. (2000), as well as extensive field observation (Davis et al. 1988; Odion et al. 1992; Odion et al. 1993) non-refractory seed may be somewhat more important in maritime vs. inland chaparral, at least among short-lived species. Conversely, for *Adenostoma,* the proportion of non-refractory seed (19%, Table 1) is in agreement with what has been found at more inland locations (Stone and Juhren 1953; Zammit and Zedler 1988).

How might having seed that is both refractory and not be a selective advantage in chaparral? By producing seed that germinates readily in the field, short-lived species may grow and reproduce throughout the fire cycle, which may be critical for them to sustain seed populations from one fire to the next (Zammit and Zedler 1988). As fire interval increases, the capability to augment the seed bank between fires will be of increasing importance to short-lived species because their seed banks will

otherwise diminish due to mortality and predation. Therefore, considering the past likelihood of relatively long fire intervals in maritime chaparral, it is not surprising that I found non-refractory seed to be so prevalent, even among fire-recruiters. It is possible that some non-refractory seed remains dormant under the chaparral canopy due to inhibitors. However, short-lived species such as *Navarettia atractyloides, Helianthemum scoparium, Chorizanthe* spp. and *Camissonia micrantha* (Sprengel) Raven are common in old age class maritime chaparral (Davis et al. 1988; Holl et al. 2000), particularly in the canopy gaps that typify this vegetation. Their seeds are concentrated in gaps, an advantage because survival with fire is much greater there (Odion and Davis 2000). The germination ecology of these and other short-lived species allows them to exploit gaps when they appear in maritime chaparral, resulting in more abundant post-fire recruitment than would otherwise occur. Such opportunistic germination has been documented in other chaparral (Zammit and Zedler 1988), and linked to canopy gaps (Shmida and Whittaker 1981), but its relative importance undoubtedly varies with chaparral canopy dynamics.

The dominant shrubs in the study, *Adenostoma, Arctostaphylos,* and the two species of *Ceanothus,* are fire-recruiters. Nearly all chaparral areas are dominated by some combination of these genera and there has been much interest in their germination ecology. For *Adenostoma,* the most widespread and abundant chaparral shrub, a question that has persisted had been, what is the role of heat in germination of refractory seed? *Adenostoma* seed banks have been studied previously by Christensen and Muller (1975) who heated soil under shrubs *in situ* Zammit and Zedler (1988, 1994) who burned straw over soil placed in flats, and Parker (1987) who oven-heated soil and supplied charred wood extract. The first two procedures enhanced germination of *Adenostoma,* but it is unclear whether this was a direct or indirect effect of heat. Parker (1987) found that charred wood extract, not heat, enhanced germination. It is possible that the heat he supplied (100°C for 1 h) was in excess of what the seeds in the samples could tolerate since it resulted in a decrease in germination. On seeds collected from shrubs, oven-heating stimulated germination (Wright 1931; Sampson 1944; Stone and Juhren 1953). In addition, Keeley (1987) found that heat alone increased germination compared to controls in 6 of 6 different temperature treatments, but there was not a statistically significant effect. However, Keeley did find significantly enhanced *Adenostoma* germination with charate, and that there was a synergistic effect with heat and charate. I also found that heat and charate produced a synergistic effect, but unlike Keeley, that germination was significantly enhanced with heat alone. It is possible that stimulatory substances were formed and/or inhibitors destroyed when I heated soils. Chemical stim-

ulants can be produced when soil or wood are heated to 175°C for 10–30 min (Keeley and Nitzberg 1984; Keeley and Pizzorno 1986). However, these stimulants are effective in very low concentrations (Keeley and Pizzorno 1986) and my heat treatment did not produce a germination effect comparable to that found with heat and charate.

In contrast to *Adenostoma,* the *Arctostaphylos* and *Ceanothus'* in this study are narrowly distributed taxa whose germination ecology has not been previously studied. However, congeneric ecological analogs can be compared. I found that heat was effective in inducing *Arctostaphylos purissima* seeds to germinate, and again that there was a synergistic effect with both heat and charate. This effect has been found in one other *Arctostaphylos* that coincidentally is also a narrow endemic from maritime chaparral, *A. morroensis* Wiesl. & B. Schreiber (Tyler et al. 1998; Tyler et al. 2000). Their methods avoided potential influence of soil-derived stimulants because seeds were extracted from the soil prior to heating. Germination doubled with heat and charate, but, there was no effect with heat alone, or charate alone. Conversely, Parker (1987) found that dormancy of *A. canescens* seeds extracted from the soil was overcome by charred wood extract alone. Freshly collected seed remained dormant with the same treatment. Other research using freshly collected seed has found that just heat (Sampson 1944; Berg 1974) or charate (Keeley 1987) can be effective in breaking seed dormancy of *Arctostaphylos.* Further research on *Arctostaphylos* spp. seed banks is needed to determine how variation in their germination may be correlated with fire regime or other environmental variables.

Ceanothus spp. have a hard seed coat that can be cracked by heat (Quick 1935; Quick and Quick 1961). There can be some germination in the absence of fire if the impermeability of the seed coat deteriorates over time (Quick and Quick 1961), e.g., *C. greggi* A. Gray, (Moreno and Oechel 1991; Zammit and Zedler 1994). In addition, Keeley (1991) reports that it is typical for a few percent of the seeds of *Ceanothus* to be non-refractory. In the stands I studied, seeds of *C. cuneatus* var. *fascicularis* and *C. impressus* had resided in the soil for a considerable length of time. Neither species was in the pre-burn vegetation in the older stand; both drop out as stands of maritime chaparral age–after only ~20 y in the case of *C. impressus* (Davis et al. 1988). Nonetheless, I found no germination of this species or *C. cuneatus* var. *fascicularis* without heat. Because input into the seed bank for these species will cease in long-unburned stands, seeds must survive and remain dormant for their seed banks to persist. These two species may have seed coats that are especially resistant to deterioration, perhaps because they are relatively thick. Thickness of seed coats is correlated with heat endurance (Wright 1931), and I found these *Ceanothus* spp. were more capable of germinating in areas of great-

er soil heating than any other species at the two burn sites (Odion and Davis 2000).

Another hard-seeded species with heat-stimulated germination was the annual *Lotus strigosus* (Table 1). It is curious that this species, unlike the *Ceanothus* spp., had germination further enhanced by heat and charate. *Lotus strigosus* was common the second spring after fire. Second year plants may have emerged from seed that did not germinate the first year, or from seed produced the first year. Charate-induced germination could allow newly produced seed to germinate the following year without heat if water soluble byproducts of wood combustion are still present in the burn area. Another hard-seeded annual legume *Trifolium microcephalum* did not have charate-enhanced germination, and the phenomenon has not been reported among other hard-seeded species (Baskin and Baskin 1998; Table 10.6).

Baskin and Baskin (1998; Tables 10.4 and 10.7) list a few chaparral species that may have germination reduced by heat or charred wood extracts. I found germination that was suppressed by heat (one species), and by heat and charate (three species; Table 1). Curiously, two of the species suppressed by heat and charate (*Crassula connata* and *Centaurium davyi*) had germination that was enhanced by heat alone. Both were uncommon in the field after fire despite having abundant seed in the soil. In fact, it was not until three to four years after each burn that *Centaurium* seedlings appeared, so the same mechanism that inhibited germination in samples apparently operated in the field. The results for *Crassula* may be at odds with what occurs elsewhere. This species is often apparent after fire in chaparral, however, this may be due to increased biomass of individuals, not increased densities.

In conclusion, seed banks in the maritime chaparral I studied may differ from most inland counterparts in the following ways: 1) greater importance of non-refractory seed, 2) lack of entirely fire-dependent germination in short-lived species, 3) germination among *Arctostaphylos* stimulated by heat and especially heat and charred wood extracts together, 4) more strongly enforced dormancy among *Ceanothus* spp. and 5) greater importance of fire-suppressed germination. Conversely, germination of the *Adenostoma* seed bank appears consistent with what occurs elsewhere. Further study of soil seed banks will be required to determine whether there has in fact been divergence in the germination ecology of maritime chaparral. In particular, it would be illuminating to directly compare seed banks of species that occur in both inland and maritime chaparral.

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HEDOSYNE (COMPOSITAE, AMBROSIINAE), A NEW GENUS FOR IVA AMBROSIIFOLIA

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ABSTRACT

Hedosyne Strother is a new genus based on *Iva ambrosiifolia* (A. Gray) A. Gray [≡*Euphrosyne ambrosiifolia* A. Gray ≡ **Hedosyne ambrosiifolia** (A. Gray) Strother]. Plants of *Hedosyne* differ from those of *Iva* s.s. in having leaves mostly alternate, leaf blades 1–3 times pinnately divided or lobed, and capitulescences paniculiform and either ebracteate or with 3–6+ heads per bract.

In morphology-based cladistic analyses of *Iva* L. and other genera of Ambrosiinae, Bolick (1983) placed *Iva ambrosiifolia* (A. Gray) A. Gray sister to *Xanthium* L. and Karis (1995) placed *I. ambrosiifolia* sister to *Euphrosyne parthenifolia* DC. (the type and only species of *Euphrosyne*). Miao et al. (1995a, b) reviewed relationships of ivas and other Ambrosiinae with respect to variations in chloroplast DNA and nuclear rDNA; they concluded that *I. ambrosiifolia* did not result from hybridization and they placed *I. ambrosiifolia* sister to *Dicoria canescens* A. Gray.

Although they differ in their placements of some species, Bolick, Karis, and Miao et al. all considered *Iva* s.l., i.e., *Iva* sensu Jackson (1960), to include species that have closer relationships outside *Iva* s.l. than within. I agree that five species (constituting *Iva* sect. *Cyclachaena* (Fresenius) A. Gray, sensu R. C. Jackson) should be withdrawn from *Iva* s.l. and I treat them as monotypic genera: *Chorisiva* Rydberg [*C. nevadensis* (M. E. Jones) Rydberg ≡ *Iva nevadensis* M. E. Jones], *Cyclachaena* Fresenius [*C. xanthifolia* (Nuttall) Fresenius ≡ *Iva xanthifolia* Nuttall], *Leuciva* Rydberg [*L. dealbata* (A. Gray) Rydberg ≡ *Iva dealbata* A. Gray], *Oxytenia* Nuttall [*O. acerosa* Nuttall ≡ *Iva acerosa* (Nuttall) R. C. Jackson], and a new genus, *Hedosyne* [see following].

Iva s.s. and the other genera may be distinguished as indicated in the following key:

1. Capitulescences racemiform or spiciform, bracteate with 1–2 heads per bract . . . . *Iva* s.s.
1. Capitulescences paniculiform, ± ebracteate or with 3–6+ heads per bract, or heads ± scattered.
2. Leaves all or mostly opposite, blades rarely lobed or divided, mostly deltate, triplinerved, and ± toothed . . . . *Cyclachaena*
2. Leaves all or mostly alternate, some or all blades ± pinnately laciniate-lobed or 1–3 times pinnately divided.
3. Plants suffrutescent or shrubby; phyllaries, paleae, and cypselae ± villous . . . . *Oxytenia*
3. Plants mostly herbs, rarely woody at base; phyllaries, paleae, and cypselae glabrous or strigillose and/or hispidulous.

4. Leaf blades laciniately lobed, the lobes mostly 3–12+ mm wide, abaxial faces ± lanate, the adaxial ± tomemtose . . . . *Leuciva*
4. Leaf blades mostly 1–3 times pinnately divided, the lobes 1–3 mm wide, abaxial and adaxial faces ± scabrellous and/or hispidulous.
5. Heads ± scattered; herbaceous phyllaries usually 3, usually longer than the florets; lobes of corollas of functionally staminate florets erect . . . . . *Chorisiva*
5. Heads in paniculiform arrays; herbaceous phyllaries usually 5, ± equalling the florets; lobes of corollas of functionally staminate florets reflexed . . . *Hedosyne*

Hedosyne Strother, gen. nov.

A *Iva* s.s. foliis pro parte maxima alternatis 1–3-pinnatis, capitulescentiis laxe paniculiformibus ± ebracteatis vel capitulis 3–6+ ad quoque bracteam, et corollis florum pistillatorum nullis differt.

Type: *Euphrosyne ambrosiifolia* A. Gray ≡ *Iva ambrosiifolia* (A. Gray) A. Gray ≡ *Hedosyne ambrosiifolia* (A. Gray) Strother.

The name *Hedosyne* comes from the Greek word hedosyne, meaning delight (see Brown 1956), and is, I believe, a suitable name for a sister or stepsister to Euphrosyne, one of the three Graces. As here circumscribed, *Hedosyne* includes a single species:

Hedosyne ambrosiifolia (A. Gray) Strother, comb. nov. Basionym: *Euphrosyne ambrosiifolia* A. Gray, Pl. Wright. 1:102. 1852, as *ambrosiaefolia*. ≡ *Iva ambrosiifolia* (A. Gray) A. Gray in A. Gray et al., Syn. Fl. N. Amer. 1(2): 246. 1884. ≡ *Cyclachaena ambrosiifolia* (A. Gray) Rydberg N. L. Britton et al., N. Amer. Fl. 33:10. 1922. —Type: western Texas or adjacent New Mexico, May–Oct. 1849, *C. Wright* "310" (GH; isotypes: UC! US).

Cyclachaena lobata Rydberg in N. L. Britton et al. N. Amer. Fl. 33:10. 1922. ≡ *Iva ambrosiifolia* (A. Gray) A. Gray subsp. *lobata* (Rydberg) R. C. Jackson, Univ. Kansas Sci. Bull. 41:838. 1960. —Type: Mexico, Nuevo León, Monterrey, Aug 1911, *Alban and Arsene 208* (US; isotype: MO).

Habit annual. **Stems** erect, 1–5(–10) dm. **Leaves** mostly alternate, petioles 5–12(–45) mm long, blades deltate or ovate to lanceolate in outline, mostly 3–5(–9) cm long, 4–5(–8) cm wide, 1–3 times pinnately divided, ultimate lobes oblong to lance-linear, 1–3 mm wide, faces scabrellous and/or hispid, usually gland-dotted. **Capitulescences** loosely paniculiform, ± ebracteate or heads 3–6+ along an axis from the axil of each bract; peduncles 3–12+ mm long. **Involucres** ± hemispheric, 2–3+ mm high. **Phyllaries** 10–12+ in 2+ series, free, the outer 5 ± herbaceous, about equalling the florets, the inner phyllaries scarious to membranous, equalling or shorter than the outer. **Pistillate florets** 5–10, corollas none. **Functionally staminate florets** 5–10(–20+), corollas funnelform, 1.5–2 mm long, the lobes soon reflexed. **Receptacles** hemispheric; paleae spatulate to linear, membranous. **Cypselae** pyriform, ± obcompressed, 1.4–1.7 mm long, finely striate, glabrous (said to become muricate in age); pappus none. $x = 18$.

Plants of *Hedosyne ambrosiifolia* usually grow in sandy, sometimes gypseous or calcareous soils, often in disturbed places (roadsides, washes, etc.) in southwestern United States (Arizona, New Mexico, Texas) and northwestern Mexico (Chihuahua, Coahuila, Durango, Nuevo León, San Luis Potosí, Sonora, Zacatecas).

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BOOK REVIEWS

2nd Interface Between Ecology and Land Development in California. Edited by J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham. 2000. U.S. Geological Survey Open-File Report 00-62. Sacramento.

This book brings together a set of papers delivered at the 2nd Interface Between Ecology and Land Development Conference held in 1997. I had the pleasure to review the proceedings from the first conference, held in 1992 (Keeley 1993), and it is interesting to observe how the issues have both developed and remained the same in the intervening time.

The issues and problems of rampaging land development and how these impact the natural environment are important virtually everywhere in the world. They are particularly acute in California, where urban development, in particular, appears to the outsider to be virtually out of control. These pressures, together with the state's biotic diversity place California as one of the biodiversity "hotspots" of the world (Myers et al. 2000) and one of the regions most likely to undergo massive biotic change (Sala et al. 2000). California is one of the few recognized hotspots in the northern hemisphere, and is unique in its position in the world economy. In few parts of the world is such exceptional affluence and quality of life set against a rich and varied natural environment and biota. California thus presents an interesting litmus test for whether we can successfully develop methods and approaches to integrating development and conservation. If California, with its affluence and relatively educated population, cannot tackle the problems effectively, what hope is there for the rest of the world, where public and private funds are scarcer and conservation ranks much lower on the list of important issues?

So this collection of papers is exceptionally interesting from an outsider's perspective. The issues discussed here, while focusing on the Californian situation, are relevant in most parts of the world. The book starts with a paper from Mike Soule, which is the transcript from his keynote address at the conference, and as such is very conversational and discursive. Soule's topic is the Wildlands Project and the need to be bold when tackling the creeping development crisis. While I'm sympathetic to his argument, I'm not sure that it does much to help the main issue of the conference. In the face of rampaging land development, it's not enough any more to say "Stop it" and seek to put as much land as possible into conservation networks. Over much of coastal California, it's too late for a Wildlands Project approach, but there is nevertheless much of conservation value that needs to be protected and managed, and much that can be done to direct and control development so that it is more ecologically acceptable.

The rest of the book tackles some key areas around this problem. The first section looks at the thorny issue of fire management along the wildland/urban interface, and the papers reflect a range of opinions and approaches. A key message in many of the papers is that prescribed fire is likely to be a key management tool, but that there are many questions and issues still to be resolved. The next section deals with habitat fragmentation and its impacts on biota, and the next with NCCP and Land Planning.

A final, long section discusses various aspects of restoration ecology, or how to repair damaged ecosystems and return species to areas of their former range. Some may view this increasing emphasis on restoration as defeatist, maintaining that the main game should still be the preservation of undamaged, pristine habitat. The unfortunate fact is that the amount of undamaged habitat remaining is declining all the time and the maintenance of some ecosystems and species demands that we take remedial action and repair some of the past damage. This series of papers represents a fine collection of current ideas and approaches in this area. I cannot agree with Peter Bowler's plea that everyone, including individuals and agencies, has to concentrate on getting to know small local areas intimately and restoring a few acres. This is fine in theory and will work in a few cases—however, it belies the immensity of the task ahead. If we are serious about broad-scale management and restoration, we will have to deal with vast areas, and this demands that we have effective, replicable treatments which can be applied over large areas. Of course, small-scale restoration is also essential as an ideal way to involve our increasingly urbanized population in contact with nature—recreating bits of nature in cities probably represents one of the best hopes for turning around our current crazy development path. This needs more emphasis on the value of city wildlife and more ecologists prepared to spend time in the cities instead of seeking out nice wild areas far away!

Overall, this collection of papers presents an interesting cross-section of current issues and approaches which should be of value to anyone with an interest in ecology and conservation in California. The coverage is inevitably variable in depth and comprehensiveness, but there is still a wealth of information here. The index is a bit if a token effort and not really very helpful, and there are a few more typos than you would expect. Perhaps the

most serious omission from the book is a synthetic chapter at the end. This would have increased the value of the book immensely. If we are to make progress in dealing with issues such as the interface between ecology and land development, we as scientists need to make sure that we ourselves interface effectively. Only by communicating clearly and concisely about these issues with the people who are making and regulating development decisions will we have any hope of changing the way things happen. Most developers and regulators will not read the papers in this book, but they are the ones that we most need to engage with. Maybe if there is to be a third conference in this series, that is the issue on which it should concentrate.

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Synthesis of the North American Flora. Version 1.0. By John T. Kartesz and Christopher A. Meacham. 1999. North Carolina Botanical Garden, University of North Carolina at Chapel Hill. In cooperation with The Nature Conservancy, NRCS, USDA, USFWS, USDI. $495.00. ISBN 1-889065-05-6.

Minimums requirements, a Pentium 90 MHz class processor, 32 MB RAM, 25 MB free hard drive space, SVGA display (minimum resolution, 800 by 600, 1280 by 1024 recommended) with 16 colors, Microsoft Windows 3.1, 95, 98, NT, or 2000 operating system, CD-ROM drive for installation.

This is a most impressive work. An update of, and an expansion on Kartesz 1994, A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland, Second edition, Volume 1, Checklist and 2, Thesaurus, Timber press, Portland. Unlike its predecessor, near-instant answers, comparisons, and analyses can be obtained to a multitude of questions within and beyond the scope of the printed work. It contains a comprehensive database with a high level of accuracy on the taxonomy, nomenclature, phytogeography, and biological attributes of the North American vascular flora

(by Kartesz) combined with highly functional software for accessing the database (by Meacham). Thus, a slick and versatile product. The cover in the jewel case is a six page insert. Included is "Nomenclatural Innovations" with 41 new combination (see International Code of Botanical Nomenclature (Saint Louis Code), 2000; Recommendation 30A.1. Ex. 1). Installation of the product is simple. The "Overview of Basic Functions" in the help menu can be printed for immediate reference or accessed as needed.

As the title indicates, this work covers North America north of Mexico. Treated are all continental states and the District of Columbia for the U.S.A., all provinces of Canada with Newfoundland displayed separate from Labrador and the Northwest Territories by administrative district (Keewatin, Mackenzie, and Franklin), the islands of St. Pierre and Miquelon, and Greenland. Furthermore, Puerto Rico, the U.S. Virgin Islands, and Hawaii are also included.

The primary screen contains three nomenclature windows on the left with lists by family, genus, infrageneric name (specific, subspecific, varietal epithets), respectively. A box above each list allows one to type the first few letters of a name and then click on it, or one can scroll and click on a name (options, with common or contrived names, authors, hybrids, synonyms, and either in checklist or thesaurus format). Or the family window can be circumvented by selecting the "All Genera" option. For the area covered, 28,033 taxa are recognized. Nearly 72,000 scientific names and synonyms and nearly 35,000 distribution maps for taxa at all ranks are included. When a taxon at any level is highlighted, its distribution appears in bright green (yellow for states where rare, pink if considered noxious, etc.) on the map in the Geography window, upper right on screen. When a unique taxon is selected, passing the cursor over a political unit or "region" within its range causes a "flyover window" to appear with indication of bibliographic reference, source of voucher, etc., on which a record is based. By highlighting a political unit under "Query," the contents of the three nomenclature windows are adjusted so as to include only the taxa documented for it. A breakdown of the included taxa may be found under "Summary" in the Attributes window, lower right on the screen. As an example, Texas with 6022 unique taxa; 199 families, 1390 genera, 5320 species, 395 subspecies, 1254 varieties, 77 hybrids for a total of 8635 taxa at all hierarchical levels.

Also in the geography window, operation buttons allow the **set union** (+) of two or more regions (e.g., union of Texas + New Mexico + Arizona) to give all taxa found therein; **set intersection** (*) for a list of taxa found, say in Colorado **as well as** Wyoming (intersection of Colorado * Wyoming); and **set subtraction** (or "**not**," −) is used to calculate the set of taxa unique to one political unit

when compared to one or more other such units (e.g., taxa found in Texas but not in New Mexico or Arizona). Also, "Composite Regions" may be used to select groups of states or provinces such as the Northeast states, the Rockies, or the Appalachians.

Also in the Attributes window, is a standard set of character states for the plant highlighted. For *Poa palustris* L., the following features appear: flowering plant, monocot, grass, perennial, native, alpine to subalpine, wetland, herbaceous, economic importance, major range plant, and occurrence (e.g., national parks and forests and all political units where documented). It is also possible to use set union, set intersect, and set subtraction in combination with a region and one or more attribute characters (e.g., intersection for California*woody*native*monocots results in 20 unique taxa). If you wish to save the results, say a search of all unique taxa with synonyms and authors by family for one or a group of states, they can readily be moved into Microsoft Word 95 or 98, Corel WordPerfect Suite 8, etc. All of the above and more. A 1 MB demonstration version for Windows may be downloaded at <http://www.bonap.org/>.

I must confess, I have had a review copy of this work on my computer for nearly a year. I have used it numerous times almost daily while working on a checklist of the vascular plants of Colorado with synonymy and on a list of exotic plants for Wyoming. Now, finally, a review.

Future plants for the Synthesis include county-level occurrence data for the U.S., illustrations and colored photos of all taxa available, and a random access key to all North American species. With Kartesz's productivity and expertise and Meacham's "magic," I anxiously await the appearance of future editions, likely on DVD.

—RONALD L. HARTMAN, Rocky Mountain Herbarium, Department of Botany, University of Wyoming, Laramie 82071-3165.

NOTEWORTHY COLLECTIONS

CALIFORNIA

ARABIS PINZLIAE Rollins (BRASSICACEAE).—Mono Co.: Inyo Nat. For., Sierra Nevada, ridge ca. 1 km ENE of Two Teats, 37°43′03″N, 119°05′35″W, elev. 3200–3280 m, krummholz woodland of *Pinus albicaulis* with *Lupinus lepidus* var. *lobbii, Leptodactylon pungens, Eriophyllum lanatum* var. *lanatum, Eriogonum ovalifolium* var. *nivale, Primula suffructescens,* etc., one colony in fine, gravelly, volcanic scree on SE-facing N slope just below ridgetop, 22 Aug. 1996, *H. Constantine-Shull 1158* (HSC). Verified by J. D. Morefield, Nevada Natural Heritage Program.

Previous knowledge. Known from 9 sites in Esmeralda Co., Nevada and 1 site in Mono Co., California at the north end of the White Mountains in granitic scree in steeply-sloped dry drainages on north to east aspects, elev. 3000–3350 m (J. D. Morefield and D. W. Taylor, Noteworthy Collections (California), Madroño 37:64–65, 1990; R. Rollins, in Hickman (ed.), The Jepson Manual, Higher Plants of California, 1993; J. D. Morefield, Status Report: Arabis pinzliae Rollins (1982, 1994), but not reported from the Sierra Nevada in these or any other available flora (e.g., A. Howald, Vegetation and Flora of Mammoth Mountain, Report for the Mammoth Mountain Ski Area, Mammoth Lakes, CA, 1983; M. Bagley, Sensitive Plant Survey for June Mountain and Rodeo Meadows, Report for the Mammoth/June Ski Resort, Inyo National Forest, Mono County, CA, 1988; N. F. Weeden, A Sierra Nevada Flora, 1996, etc.).

Significance. First record of the species from the Sierra Nevada. A range extension of ca. 78 km WSW from the Boundary Peak region in the White Mountains. This record may suggest a possibly very recent Sierran origin for this newly developed taxon (H. Constantine-Shull, Floristic Affinities of the San Joaquin Roadless Area, Inyo National Forest, Mono County, CA, 2000). Plants in the Sierran population fit *A. pinzliae* morphological characteristics; however, 2 out of the 15 plants measured had mature fruits 0.5 mm longer than expected for the taxon. Further analyses on this Sierran population may help to clarify the taxon's distinction from *A. platysperma* A. Gray var. *platysperma. Arabis pinzliae* should be sought at additional locations in the central-eastern Sierra, especially on adjacent ridges, and in the Glass Mountains ca. 38 km ENE of the Sierran population where there appears to be suitable habitat.

ARTEMISIA MICHAUXIANA Besser (ASTERACEAE).— Mono Co., Sierra Nevada, streamside ca. 1.75 km E of Inyo Crater Lakes, 37°42′N 119°02′W, elev. 2500 m, *Abies magnifica* var. *magnifica* forest with *Pinus contorta* subsp. *murrayana* Critchfield, in gravelly pumice soil in a wet area along a stream with *Salix lemmonii, Carex nervina, Cicuta maculata* var. *angustifolia, Epilobium ciliatum* subsp. *ciliatum,* etc., 28 Jul. 1996, *H. Constantine-Shull 987* (HSC); Moist pumice soil beside Deadman Creek ca. 2.25 km E of Two Teats, 37°42′N 119°04′W, elev. 2680 m, open avalanche zone with *Artemisia tridentata* subsp. *vaseyana, Populus tremuloides, Salix lemmonii, Delphinium glaucum,* 1 Sept. 1996 *H. Constantine-Shull 1180* (HSC).

Previous knowledge. In subalpine to alpine scree, talus, and drainages in the White and Inyo Mountains and in the Marble Mountains of the Klamath Region, north to B.C., Montana, Colorado (L. Abrams and R.S. Ferris, Illustrated Flora of the Pacific States, WA, OR, and CA, Vol. IV, 1960; P.A. Munz, Supplement to A California Flora, 1968; L.M. Shultz in Hickman (ed.) The Jepson Manual, Higher Plants of California, 1993) but not reported from the Sierra Nevada in these floras or by any specimen recorded in the Cal Flora database, 1999. One undocumented sighting with no specimen was noted in Glacier Canyon in Yosemite (J. T. Howell, A list of the vascular plants of Tuolumne Meadows and vicinity, Sierra Club Nature Notes #13, 1944). This may be the reference to a Sierran range for this plant in A. Cronquist et al. Intermountain Flora Vol. 5—Asterales, 1994.

Significance. First documented report of the species from the Sierra Nevada. A range extension of ca. 75 km from the Montgomery Peak region of the White Mountains. These eastern Sierran populations occur at lower elevations (2500–2680 m) than the 3000 m minimum elevation recorded by the Jepson Manual and specimens cited in the Cal Flora database.

ARTEMISIA LUDOVICIANA Nutt subsp. *CANDICANS* (Rydb.) Keck (ASTERACEAE).—Mono Co., Sierra Nevada, Minaret Meadow ca. 1 km E of Minaret Summit, 37°39′27″N, 119°02′52″W, elev. 2690 m, in gravelly pumice soil along streamside in and below the meadow with *Pinus contorta* ssp. *murrayana, Salix lemmonii, Lonicera involucrata* var. *involucrata, Arabis holboellii* var. *pinetorum,* 20 Aug. 1996 *H. Constantine-Shull 1224* (HSC).

Previous knowledge. In dry woodland, shrubland from the northern Sierra Nevada and Modoc Plateau to Washington, Montana, and Utah (L. Abrams and R. S. Ferris, Illustrated Flora of the Pacific States, WA, OR, and CA, Vol. IV, 1960; L. M. Shultz in Hickman (ed.) The Jepson Manual, Higher Plants of California, 1993; A. Cronquist et al. Intermountain Flora Vol. 5—Asterales, 1994; Cal Flora database, 1999).

Significance. First report of the subspecies for Mono County. A range extension of ca. 222.6 km SSE from Donner Pass Ridge, Nevada Co., CA (Cal Flora database).

—HELEN CONSTANTINE-SHULL, 825 UNION STREET, ARCATA, CA 95521 AND JOHN O. SAWYER, JR., Dept. of Biology, Humboldt State University, Arcata, CA 95521.

These findings are presented in Constantine-Shull, H. 2000. Floristic Affinities of the San Joaquin Roadless Area, Inyo National Forest, Mono County, California. M.A. thesis. Humboldt State University, Arcata, CA.

The thesis is also published with University Microfilms, Incorporated.

A California Native Species Field Survey Form for *Arabis pinzliae* has been submitted to the Natural Diversity Data Base, California Department of Fish and Game.

CALIFORNIA

LIQUIDAMBAR STYRACIFLUA L. (HAMAMELIDACEAE)—Sacramento County, on the north bank of the American River in the American River Parkway, a few hundred meters downriver of the Estates Drive entrance,

N38°33′, W121°22′, 16 June 1998, *J. M. Randall s.n.* (DAV). A fruiting tree was found growing along the river in this semi-wild preserve bordered by residential areas. The tree appears to be a naturalized specimen, but it is possible that it was planted and then neglected. The narrow strip of forested land along the river where the tree occurs is dominated by *Quercus lobata, Populus fremontii, Fraxinus latifolia,* and *Acer negundo* var. *californicum* and the exotic *Sapium sebiferum.* Prominent understory plants include *Toxicodendron diversilobum* and numerous exotics including *Arundo donax, Conium maculatum, Raphanus raphanistrum, Rubus discolor, Saponaria officinalis,* and *Vinca major.*

Previous knowledge. Native to the eastern North America, from Connecticut to southern Illinois and south to Florida, west to Oklahoma and south again to eastern Mexico and Guatemala (H.A. Gleason and A. Cronquist 1991, Manual of Vascular Plants of Northeastern United States and Adjacent Canada. New York Botanical Garden, NY). This species, commonly called sweet gum, is commonly cultivated as an ornamental tree, and widely recognized for its unusual spiky-spherical fruits, beautiful 3 to 7-pointed leaves, and fall color. Many cultivars and hybrids have been developed with the other two species of *Liquidambar* that are native to Asia (A. L. Jacobson 1996. North American Landscape Trees. 10 Speed Press, Berkeley, CA). Its wood is valued for furniture, flooring and veneer. Reported as growing wild outside of its original range in a large population at one site in northeastern Illinois (F. Swink and G. Wilhelm. 1994. Plants of the Chicago Region. 4th edition. Indiana Academy of Science, Indianapolis).

Significance. First record in California. We know of no other reports of establishment of *L. styraciflua* west of its native range despite widespread cultivation of the species in low elevation areas of the western U.S. We have also been unable to find reports of *L. styraciflua* escaping cultivation on other continents.

SAPIUM SEBIFERUM (L.) Roxb. (EUPHORBIACEAE).—Sacramento County, on the north bank of the American River in the American River Parkway, a few hundred meters downriver of the Estates Drive entrance, N38°33′, W121°22′, 28 June 1998, *B. A. Meyers-Rice #MR980603* (DAV). Approximately two dozen semi-mature trees were found growing along the river in a wildland preserve bordered by residential areas. Numerous seedlings have also been found on sandbars along the river. The narrow strip of forested land along the river is dominated by *Quercus lobata, Populus fremontii, Fraxinus latifolia,* and *Acer negundo* var. *californicum.* Prominent understory plants include *Toxicodendron diversilobum* and numerous exotics such as *Arundo donax, Conium maculatum, Raphanus raphanistrum, Rubus discolor, Saponaria officinalis,* and *Vinca major.*

Previous knowledge. Native to China. *Sapium sebiferum* (Chinese Tallow Tree) was introduced to the east coast of the USA in the late 1700s. It now occurs in every coastal state from North Carolina to south Texas, inland to Arkansas, and in Florida as far south as Tampa; overseas it has escaped cultivation in Japan, Formosa, India, Pakistan, central and southern Europe, Martinique, and the Sudan (K. A. Bruce, et al. Natural Areas Journal, 17:255–260, 1997). *Sapium sebiferum* is used in China as a source of soap and other products, and was introduced to the USA as a potential oilseed crop. In California it is used as a landscape tree and is valued for its attractive habit,

glossy green foliage that turns red in the fall, and showy white seeds.

Significance. First record in a California wildland. The parent stock for these plants may be landscape trees from the surrounding suburbs. *Sapium sebiferum* has been seen in two other wildland locations in Placer County, at Antelope Creek and at Strap Ravine (D. Bishop, pers. comm.). The closest documented occurrence of *Sapium sebiferum* outside of cultivation is in coastal Texas, approximately 2600 km distant. This species has great potential to become a serious weed in riparian forests of California's Central Valley. Birds, especially finches and warblers, feed upon the seed and may help to spread the fruit (personal observation). Seed can also be transported by water.

SESBANIA PUNICEA (Cav.) Benth. (FABACEAE).—Sacramento County, on the margins of William B. Ponds wetland in the American River Parkway on the north side of the River at the Arden Way entrance, N38°33′, W121°22′, 28 June 1998, *B. A. Meyers-Rice #MR980604* (DAV). Large numbers of plants, ranging in age from seedlings to mature, fruiting specimens, were found growing on the margins of the pond. This pond is a heavily developed fishing pond within the American River Parkway's wildland area. Various sized specimens were also established at the low flow edges of the American River, especially on islands in the middle of the river. Total distribution in the parkway is from Ancil Hoffman Park downstream to the California Exposition floodplain.

Previous knowledge. Native to South America (Argentina, Brazil, Paraguay, and Uruguay). As an exotic species in the USA, it occurs from northern Florida and southern Georgia to eastern Texas. Previously known in California at only a few sites in Butte County (V. Oswald and L. Ahart, 1994. Manual of the Vascular Plants of Butte County, California. California Native Plant Society. Sacramento). It has been seen the area of Suisun Marsh in the California Delta, but has apparently been eradicated from this location (A. Shapiro, pers. comm.). Another location in northern Sacramento County is along Dry Creek within the Cherry Island Golf Course (R. Robison, personal communication). In southern Africa it is a serious weed in South Africa (Natal, Transvaal, and Cape Provinces), Lesotho, and Zimbabwe. *Sesbania punicea* is widely used as an ornamental plant because of its attractive compound leaves, bright sprays of red flowers and persistent winged fruit. The species *Sesbania tripetii* is closely related, and indeed may also be a synonymous name. The name "*Daubentonia punicea*" is also a synonym.

Significance. The first collection for Sacramento county. Other than the Butte County locations, the closest reported occurrence of *Sesbania punicea* is in far-eastern Texas. It is unclear how this plant was transported to California. It is likely to become a serious weed in the riparian areas of California's Central Valley. It forms dense thickets, especially in moist areas, in the southeastern USA and southern Africa. Its seeds are effectively transported by water.

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Sonora, Mexico

Salvia similis Brandegee (LAMIACEAE).—Municipio de Guaymas, peninsula at S side of Algodones Bay, 2 km W of Cerro Tetas de Cabra summit, 27.9°N, 111.0°'W, north-facing granite slope, elev. 5–20 m, desertscrub with *Stenocereus thurberi, Jatropha cuneata, Bursera microphylla, Fouquieria diguetii*; uncommon shrubs, about 1 m tall, 17 March 1983, *Burgess 6361 et al.* (ARIZ).

Significance. First record for mainland Mexico.

Previous knowledge. Otherwise known from Baja California Sur (I. L. Wiggins, *In*, F. Shreve & I. L. Wiggins, part 2, 1964 Stanford Univ. Press) where it is rather widespread and Isla San Pedro Nolasco (R. S. Felger and C. H. Lowe, Natural History Museum of Los Angeles County, Contributions in Science 285, 1976).

Notes. Apparently rare on the mainland although common on Isla San Pedro Nolasco on east-facing slopes near the summit. Both of these populations are on north- and east-facing granite slopes above the sea; there are very few mainland habitats where these conditions are duplicated.

Eragrostis spicata Vasey *(POACEAE)*.—Municipio de Guaymas: Bahía San Carlos, Crestón area, ca. 3 m elev., disturbed habitat, 8–10 m N of highway, among *Prosopis glandulosa*, perennial, forming dense clumps ca. 1–1.5 m tall, colony of dozen or so plants, 18 November 1984, *Felger 84–544 & Valdez Zamudio* (ARIZ, MEXU, TEX); 20 March 1986, *Felger 86–67 & Sanders* (ARIZ). Mex Hwy 15, 1.7 mile SE of Pitahaya (Belem, Río Yaqui) junction, elev. 10 m, 27°45'N, 110°24'W, coastal thornscrub, pond near roadside, densely shaded by *Prosopis glandulosa;* robust grass to 1.8 m tall, 11 October 1985, *Felger 85–1248 & Reichenbacher* (ARIZ, MEXU). Mex Hwy 15, 3.6 mile S of Pitahaya (Belem, Río Yaqui) junction, ca. 10 m, 27°42½'N, 110°22'W, in shade of mesquites; common robust perennial to 1 m tall, 11 October 1985, *Felger 85–1248 & Reichenbacher* (ARIZ, MEXU). Municipio de Hermosillo: Hwy 24, 5.0 mile N of Sahuaral (4.7 mile N of Bahía San Agustín Rd junction), elev. 5 m, 28°23'N, 111°21'W; low lying, temporarily swampy area; fine-textured silty-muddy soil; shallow standing water in lowest areas; shade of mesquite; common, 12 October 1985, *Felger 85–1586 & Reichenbacher* (ARIZ, MEXU).

Significance. First record for Sonora.

Previous knowledge. Texas, northeastern Mexico, Baja California Sur, and Argentina and Paraguay (F. W. Gould and R. Moran, San Diego Society of Natural History Memoir 12, 1981; F. O. Zuloaga, et al. Monographs in Systematic Botany from Missouri Botanical Garden 47, 1994).

Notes. This large, perennial grass is a common and consistent element in the grassy, savanna-like swampy habitats of coastal west-central Sonora between the Río Yaqui and Empalme (southeast of Guaymas), with outlier populations at San Carlos north of Guaymas and near Sahuaral (east of Tastiota). The plants are reproductive at least in March and November. In west-central Sonora it often grows beneath mesquite (*Prosopis glandulosa* var. *torreyana*) with *Kosteletzkya hispidula, Luffa operculata* var. *intermedia, Phyllanthus evanescens, Sesbania herbacea,* and grasses including *Echinochloa crusgalli, Leptochloa fusca* ssp. *uninervia, L. panicea* ssp. *brachiata, L. viscida, Panicum hirticaule* and *Sporobolus airoides.*

Portulaca johnstonii J. Henrickson *(PORTULACACEAE)*.—Municipio de Guaymas, 0.5 km W of Estero Soldado at ca. 1 km inland from shore (ca. 6 km E of Bahía San Carlos), ca. 2 m elev., coastal desertscrub, sandy soil, locally common, 18 November 1984, *Felger 84–421 & Valdez Zamudio* (ARIZ, MEXU, TEX).

Significance. New record for Sonora and the Sonoran Desert.

Previous knowledge. Known only from the type collection in Coahuila in the Chihuahuan Desert (J. Henrickson, Madroño 28:78–79, 1981).

Notes. No differences were noted between the Sonoran and Chihuahuan plants. The Sonora collection was made in an area of natural vegetation but near disturbed habitats in an area rapidly being urbanized. Immature seeds are reddish (rust-colored) throughout, the body becomes iridescent blackish with maturity. Due to the radiating fimbriae on the seeds, unique in the genus, this plant is hereby given the common name 'Punk Portulaca' (Fig. 1). It would be interesting to study the origin and development of these fimbriae; the plants are otherwise similar to *P. oleracea.*

Ximenia parviflora Benth. var. *glauca* DeFilipps *(OLACACEAE)*.—Municipio de Guaymas: Cañón La Pintada, large riparian canyon ca. 4 mile E of La Pintada (ca. 33 mile S of Hermosillo on Mex Hwy 15), riparian desertscrub, on slopes of canyon side, not common, flowers dull yellow, *Felger 3267* (ARIZ). Broad spiny shrubs ca. 1.5 m tall, apparently evergreen, herbage with a reddish cast; flowers dull yellow, the calyx red, the petals densely pubescent inside with many whitish and flattened hairs; flowering late May.

Significance. First record for this genus in Sonora.

Previous knowledge. Known only from Baja California Sur.

Notes. A unique feature of this genus is the corolla, comprised of 4 or 5 free petals densely covered inside with hairs. These hairs are said to be brownish and barbed; in the Sonoran specimen the hairs are whitish when fresh but become brownish with age, and I do not find barbed hairs on these specimens, or those from Baja California Sur, or the half dozen specimens of *X. americana* at ARIZ.

A previous collection from Baja California Sur (*Johnston 3718;* I. M. Johnston, Proceedings, California Academy of Sciences (4) 12:951–1218, 1924), misidentified as *X. pubescens* seems to be the source of the erroneous reference to *X. pubescens* in Baja California (I. L. Wiggins, Flora of the Sonoran Desert, *loc. cit.*; I. L. Wiggins, Flora of Baja California, 1980 Stanford Univ Press).

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Arizona and Sonora

Vauquelinia californica subsp. *sonorensis* Hess & Henrickson (Rosaceae).—SONORA: Municipio de Gen. Plutarco Elías, Sierra Cubabi, middle-elevation on north-facing drainage; on granite with *Dodonaea viscosa, Eriogonum* sp., *Galium stellatum, Solanum hindsianum,* vicinity 31°43'25"N, 112°50'50"W, elev. ca. 750 m, shrub ca. 8 ft tall, 11 November 1998, *Pate s.n.* (ARIZ). [Sierra Cubabi] N 35 11 000 E, 3 27 500, ca. 700 m SE of highest point in area, 1130 m elev., granite with *Stenocereus thurberi, Justicia californica, Ferocactus covillei, Eriogonum wrightii, Encelia farinosa,* scattered locally in protected areas, 19 March 1991, *Baker 8130 & Johnson* (ASU).—ARIZONA: Maricopa County, Barry M. Goldwater Airforce Range, Sand Tank Mountains, 32°39'43.3"N,

112°19′51.2″W, 2800 ft, NE-facing steep rhyolite slope; uppermost elevational limit of Sonoran Desert including *Acacia greggii, Anisacanthus thurberi, Calliandra eriophylla, Carnegiea gigantea, Cercidium microphyllum, Coursetia glandulosa, Encelia farinosa, Ephedra aspera, Eriogonum fasciculatum, Fouquieria splendens, Lycium parishii, Olneya tesota, Opuntia chlorotica, Prosopis velutina, Viguiera parishii, Yucca arizonica,* 10 October 1995, *Felger 95–337, Wilson, Smith, & Speich* (ARIZ). Sand Tank Mountains, 2 mile SW of Squaw Tit Peak, along rocky drainage with *Juniperus,* 3200 ft, 1 January 1995, *Malusa s.n.* (ARIZ).

Previous knowledge. Documented only from the Ajo Mountains in Organ Pipe Cactus National Monument, Pima County, Arizona, and disjunct in local areas on the eastern slopes of the Sierra Juarez in northern Baja California (W. J. Hess and J. Henrickson, Sida 12:101-163, 1987).

Significance and natural history notes on the species in Sonora. First record for this distinctive subspecies from mainland México and the second documentation of an Arizona population. Sierra Cubabi in Sonora is the nearest range to the Ajo Mountains, and ca. 30 km directly southsouthwest from it. The Sand Tank Mountains in Arizona are ca. 54 km northeast of the Ajo Mountains. The Sonora and Ajo Mountain populations are within the Sonoran Desert, the Sand Tank Mountain population is mostly at the upper elevational limit of the desert. All three mountains support Sonoran Desert species to their summits.

A locality mapped by Turner, et al. (Sonoran Desert Plants: an ecological atlas, 1995, Univ. of Arizona Press) as a "sighting" west of the Ajo Mountains, in Yuma County, is presumed to be erroneous.

Of the four subspecies of *V. californica,* only subsp. *pauciflora* was known for certain from Sonora (Hess and Henrickson, 1987). In Sonora it is documented from canyons and slopes at the north end of the Sierra el Tigre, at 1140 m, where it is apparently quite rare. The several collections at ARIZ are probably taken from the same one or two shrubs. The substrate is rhyolite although limestone intrusions occur nearby. Here *Vauquelinia* occurs at the upper margin of Sonoran desertscrub merging to thornscrub and just below the oak zone (*Quercus oblongifolia*). Associated plants include *Coursetia glandulosa, Dodonaea viscosa, Fouquieria splendens, Fraxinus gooddingii, Hechtia montana, Juglans major, Prosopis velutina, Rhus microphyllum,* and *Yucca arizonica.* Elsewhere this subspecies is known from limestone substrate in ecotone of Chihuahuan desertscrub and oak woodland, and lower elevations in oak woodland.

Subspecies *californica* occurs in both states of Baja California and southern Arizona including the Baboquivari Mountains near the Sonora border. It should be sought in nearby north-central Sonora. An observation of rosewood in the Sierra del Viejo near Caborca (Turner et al. 1995, *loc. cit.*) may be this subspecies or subsp. *sonorensis.*

While admiring *V. californica* subsp. *sonorensis* on a field trip of the Arizona Native Plant Society to Alamo Canyon in the Ajo Mountains, Felger suggested that it should be sought in mountains in northwestern Sonora east of Sonoyta such as the Sierra Cubabi, mountains that have scarcely been botanically explored. Pate replied that she had indeed seen it there, and soon thereafter verified it with the record cited here. Subsequently Felger located the Baker specimen at ASU.

The paucity of records for *V. californica* in northern Sonora seems unusual given its widespread occurrence and diversity (three subspecies) in adjacent southern Arizona. In view of the discovery of the Sierra Cubabi population, it seems that absence of records in much of northern Sonora for many other species likewise may be due to a lack of botanical exploration in remote and now often dangerous borderland territory. Distant areas are often far better known (e.g., Martin, Yetman, Fishbein, Jenkins, Van Devender, and Wilson, 1998, Gentry's Río Mayo Plants, University of Arizona Press).

Hess and Henrickson (1987) give a maximum size of 10 m for any *Vauquelinia,* 8 m for any of the four subspecies of *V. californica,* and 7 m for subsp. *sonorensis.* A tree in Alamo canyon, in the Ajo Mountains, carefully measured by Robert Zahner and associates (National Register of Big Trees, 1996, American Forests, Washington, D.C.) was 14.3 m (47 ft) in height with an average crown spread of 12.2 m (40 ft), and 2.0 m (78 inch) in girth at 1.4 m (4.5 ft) above ground level (original measurements in English units). Thus the most xeromorphic taxon (Hess and Henrickson 1987) in the genus contains the largest-sized individual.

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OREGON

MYRIOPHYLLUM USSURIENSE (Regel) Maxim. (HALORAGACEAE).—Clatsop Co.: Columbia River, Cathlamet Bay, Lewis and Clark National Wildlife Refuge, Russian Island, 4 miles WNW of Knappa, T8N, R8W, Sec. 11. On mud along tidal channels, subject to daily freshwater tidal inundation. 14 August 1992. *J.A. Christy 8205* (MO, NY, OSC, V).

Previous knowledge. Taiwan, China, Japan, Russian Far East, British Columbia. First reported from North America by Ceska et al. (Brittonia 38:73–81, 1986), it is known from over a dozen sites in southern British Columbia, including Vancouver Island, with the earliest collection dating from 1916. This is one of two collections from the estuary of the Columbia River of Oregon and Washington. Both sexes of *M. ussuriense* are present in British Columbia, but no flowers were found in either of the U.S. populations. We consider it to be a rare native species with an amphi-Beringian distribution.

Significance. New to the United States; new to Oregon.

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WASHINGTON

MYRIOPHYLLUM USSURIENSE (Regel) Maxim. (HALORAGACEAE).—Wahkiakum Co.: Columbia River, Julia Butler Hansen National Wildlife Refuge, small wetland across Steamboat Slough from Price Island, T9N, R6W, Sec. 16. On mud along Steamboat Slough, subject to daily freshwater tidal inundation. 29 July 1992. *J. A. Christy 8164* (WSU).

Previous knowledge. See report above for Oregon.

Significance. New to the United States; new to Washington.

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OREGON

CAREX LONGII Mack. (Cyperaceae).—Clatsop Co., wet, peaty cranberry field, 1.6 air km SSW of Cullaby Lake, Delmoor Loop Rd., elev. 4 m, T7N R10W S27, 2 Oct. 1999, *Zika 14470* (MICH, OSC, WTU).

Previous knowledge. Native to eastern North America, west to Texas. A member of the *Carex straminea* complex in *C.* section *Ovales.* For an identification key to the species, see Rothrock *et al.* (Canadian Journal of Botany 75: 2177–2195, 1997). Long's sedge is a common adventive in cultivated cranberries in New England. The seeds of this and other cranberry weeds were apparently introduced on the Pacific coast by the transport of *Vaccinium macrocarpon* vines between agricultural areas.

Significance. First report for Oregon.

CHAENOMELES SPECIOSA (Sweet) Nakai (ROSACEAE).—Jackson Co., spreading from cultivation to roadside ditches, ca. 25 seen, Applegate River valley ca. 12 air km NNE of dam at Applegate Reservoir, elev. 546 m, T39S R3W S28, 23 May 1991, *Zika 11122* (OSC).

Previous knowledge. Native to eastern Asia, and an occasional weed in eastern North America, W to Wisconsin. Flowering quince is a common ornamental in western OR.

Significance. First record as an escape from cultivation in Oregon.

COTONEASTER HORIZONTALIS Decne. (Rosaceae).—Lane Co., naturalized in Willow Creek Natural Area, with *Fraxinus, Populus, Crataegus,* West Eugene, elev. 122 m, T18S R4W S3, 9 July 1998, *Voss 1936* (OSC); Tillamook Co., bird-sown weed in grassland, S aspect, Cascade Head, elev. 275 m, T6S R11W S14, 14 Aug. 1986, *Zika 9989* (WTU).

Previous knowledge. Native to China and planted for ornament W of the Cascades. Rock cotoneaster fruits heavily in autumn, and birds such as American robins (*Turdus migratorius*) are commonly observed eating the colorful fruit and dispersing the seed of this and other *Cotoneaster* species.

Significance. First report as a wild plant in Oregon.

COTONEASTER LACTEUS W. W. Sm. (ROSACEAE).—Curry Co., bird-sown weed in roadside thickets, Route 101, Winchuck, T41S R13W S23, 24 Oct. 1990, *Zika 11024* OSC; roadside thickets, Route 101, Brookings, T41S R13W S5, 24 Oct. 1990, *Zika 11033* (OSC); Lane Co., weed in *Quercus garryana* woods, Morse Ranch, Eugene, elev. 120 m, 3 Dec. 1999, *R. Love 9962* (WTU).

Previous knowledge. Late cotoneaster is native to China, commonly planted W of the Cascades, and known to be invasive.

Significance. First report as a garden escape for Oregon.

COTONEASTER SIMONSII Baker (Rosaceae).—Coos Co., edge of coniferous woods, Route 101 near Saunders Lake, elev. 24 m, T23S R13W S35, 8 Sept. 1999, *Zika 14322* (WTU); Curry Co., roadside thicket, Route 101, Winchuck, T41S R13W S23, 24 Oct. 1990, *Zika 11025* OSC;

Tillamook Co., steep bank, Route 101, Nehalem, elev. 15 m, T3N R10W S27, 17 Sept. 1999, *Zika 14365* (WTU).

Previous knowledge. Native to the Himalayas, Himalayan cotoneaster is commonly planted as an ornamental in western Oregon, Washington, and British Columbia.

Significance. First report for Oregon as a garden escape.

ELEOCHARIS QUADRANGULATA (Michx.) Roem. & Schult. (CYPERACEAE).—Lane Co., large clone, long-established but local weed, wetland clay soil, full sun, with *Ludwigia palustris, Eleocharis palustris, Juncus marginatus, Ventenata dubia,* degraded wet prairie by abandoned airport runway and old race track, West Eugene, elev. 117 m, T17S R4W S33, 8 July 1997, *Alverson & Zika 13225* (OSC).

Previous knowledge. Native to eastern North America, west to Texas. Square-stemmed spike-rush is considered native in California.

Significance. First report for Oregon, but surely adventive, not native, on this site with a history of decades of disturbance in the industrial zone of Eugene.

HYPERICUM MAJUS (A. Gray) Britton (CLUSIACEAE).—Clatsop Co., cranberry field, with *Juncus canadensis,* Delmar Loop Rd., elev. 4 m, T7N R10W S22, 2 Oct. 1999, *Zika 14450* (OSC, WTU); Coos Co., cranberry field, with *Juncus pelocarpus,* Randolph Rd., 6 km N of Bandon, elev. 52 m, T28S R14W S4, 7 Sept. 1999, *Zika 14249* (WTU).

Previous knowledge. Greater Canadian St. Johnswort is native to wetlands across northern North America, including British Columbia & Washington. However, a number of Pacific coast populations are adventive, in gravel pits, railroad yards, and cranberry farms, where they were undoubtedly introduced from eastern cranberry states, along with *Hypericum boreale, H. canadense, H. ellipticum,* and *Triadenum fraseri.*

Significance. First report for Oregon. All known populations are weeds in agricultural settings, and are adventive, not native.

LUZULA ARCUATA (Wahlenb.) Swallen subsp. *UNALASCHCENSIS* (Buchenau) Hultén (Juncaceae).—Hood River Co., wet sunny mossy banks of Lost Lake, elev. ca. 1000 m, 29 June 1924, *Henderson 778* (ORE).

Previous knowledge. Circumboreal and native, curved woodrush is known from collections in Washington on Mt. Rainier and Mt. Adams, 85 km N.

Significance. First report for Oregon.

LUZULA FORSTERI (Sm.) DC. (JUNCACEAE).—Marion Co., lawn, Salem, Apr. 1910, *Peck 5135* (WILLU).

Previous knowledge. Southern woodrush is native to Europe.

Significance. First report for Oregon. Perhaps only a waif, but should be sought in the Salem area again.

POLYGONUM SAGITTATUM L. (POLYGONACEAE).—Clatsop Co., common, ditches and marshy borders of cultivated cranberry field, with *Carex chordorrhiza, Juncus brevicaudatus,* Delmar Loop Rd., elev. 4 m, T7N R10W S22, 2 Oct. 1999, *Zika 14459* (OSC, WTU).

Previous knowledge. Native to eastern North America, west to Colorado. Arrow-leaf tearthumb is weedy in cultivated cranberry fields in Massachusetts (Sears et al. An Illustrated Guide to the Weeds of Cranberry Bogs in Southeastern New England, 1996).

Significance. First report for Oregon.

ZANTEDESCHIA AETHIOPICA (L.) Spreng. (ARACEAE).—Curry Co., steep W aspect, base of eroding sea bluffs,

with *Holcus lanatus, Equisetum telmateia,* Nesika Beach, elev. 5–30 m, T35S R15W S36, 20 May 1997, *Zika 13085* (OSC).

Previous knowledge. Native to Natal, and a weed in California. Altar lily was originally planted on a blufftop as an ornamental, and subsequently dropped downslope as erosion undermined garden areas. Persisting for many years and spreading across a sandy precipice, despite control efforts.

Significance. First report as an escape from cultivation in Oregon.

WASHINGTON

BERBERIS DARWINII Hook. (BERBERIDACEAE).— Grays Harbor Co., steep shrubby slope, with dense *Rubus armeniacus, Lonicera involucrata, Rubus spectabilis,* N aspect, above Route 105 near Bigelow Rd., S of Aberdeen city limits, elev. 15 m, T17N R9W S20, 25 April 1998; *Zika 13422* (WTU).

Previous knowledge. Native to Chile and commonly cultivated at low elevations in western Oregon and Washington. Darwin's barberry is naturalized on the coast of Coos Co., Oregon, 400 km to the south.

Significance. First record as a wild plant in Washington.

CALLUNA VULGARIS (L.) Hull (ERICACEAE).—Pacific Co., sandy cranberry field, with *Lythrum portula, Bidens tripartita,* Pioneer Rd., 2.5 km NE of Long Beach, elev. 5 m, T10N R11W S10, 31 Aug. 1999, *Zika 14200* (WTU).

Previous knowledge. A common ornamental west of the Cascades in the Pacific Northwest. Heather is a weed on peaty soils and in cranberry farms in S British Columbia, 300 km N.

Significance. First report as an escape from cultivation in Washington.

CAREX LONGII Mack. (CYPERACEAE).—Grays Harbor Co., cranberry fields and drainage ditches, with *Juncus effusus,* 1 km N of County Line Rd., elev. 5 m, T15N R11W S7, 29 Sept. 1998, *Zika 13641* (WTU); Pacific Co., ditch in cranberry field, with *Lysimachia terrestris,* Pioneer Rd. 7 km N of Ilwaco, elev. 5 m, T10N R11W S10, 12 Sept. 1998, *Zika 13592* (WTU); peaty disturbed ground, with *Ledum groenlandicum,* near Jim Street, 2 km NE of Seaview, elev. 5 m, T10N R11W S22, 31 Aug. 1999, *Zika 14193* (WS).

Significance. First report for Washington.

COTONEASTER DIELSIANUS E. Pritz. ex Diels (ROSACEAE).—King Co., *Thuja* hedge, campus of Univ. of Washington, Seattle, elev. 25 m, T25N R4E S16, 6 Nov. 1999, *Zika 14707* (WTU); Kitsap Co., woods near New Brooklyn Rd., Bainbridge Is., Puget Sound, elev. <100 m, T25N R2E S21, 28 Sept. 1999, *Zika 14426* (US, WTU); Pacific Co., sandy edge of coniferous woods, NE of Black Lake, elev. 5 m, T10N R11W S28, 30 Sept. 1999, *Zika 14436* (WTU).

Previous knowledge. Diels' cotoneaster is native to China, and planted for its ornamental fruit west of the Cascades.

Significance. First report as a naturalized plant in Washington.

COTONEASTER FRANCHETII BOIS (ROSACEAE).—Grays Harbor Co., thickets, with *Picea sitchensis, Rubus armeniacus,* Route 105, E of Ocosta, elev. 10 m, T16N R11W S22, 19 Oct. 1998, *Zika 13650* (WTU); King Co., thickets,

Burbank Park, Mercer Is., Lake Washington, elev. 6 m, T24N R5E S6, 6 Oct. 1999, *Zika 14537* (WTU); San Juan Co., edge of forest, near pond on Turn Point, with *Symphoricarpos,* San Juan Is., Puget Sound, elev. 8 m; T35N R2W S18, 24 Oct. 1999, *Zika 14643* (WTU).

Previous knowledge. Native to China, commonly cultivated west of the Cascade Mtns. in the Pacific States. Franchet's cotoneaster is naturalized in western Oregon and coastal California.

Significance. First record as a garden escape in Washington.

COTONEASTER LACTEUS W. W. Sm. (ROSACEAE).— Grays Harbor Co., gravel roadbank, Route 109, NW of Chenois Cr., elev. 20 m, T18N R11W S15, 4 Oct. 1999, *Zika 14517* (WTU); King Co., cracks in asphalt parking lot, Mercer Middle School, S Oregon St., Seattle, elev. 30 m, T24N R4E S16, 25 Sept. 1999, *Zika 14413* (WTU).

Significance. First report as a garden escape for Washington.

COTONEASTER REHDERI Pojark. (ROSACEAE).—King Co., shade of *Pseudotsuga,* Alder Crest School, 195th St NE, elev. < 50 m, T26N R4E S4, 25 Sept 1999, *Zika 14414* (WTU); Kitsap Co., woods near Gazzam Lake, Bainbridge Is., Puget Sound, elev. 90 m, T25N R2E S29, 28 Sept 1999, *Zika 14424* (OSC).

Previous knowledge. Bullate cotoneaster is native to China, and introduced as an ornamental west of the Cascades.

Significance. First report as a wild plant in Washington.

COTONEASTER SIMONSII Baker (ROSACEAE).—Grays Harbor Co., roadsides, with *Alnus rubra, Tsuga heterophylla,* Route 105 E of Ocosta, elev. 15 m, T16N R11W S11, 16 Sept. 1999, *Zika 14341* (WTU); King Co., open forest, Lincoln Park, 0.5 km N of Point Williams, Seattle, elev. 45 m, T24N R3E S26, 14 Sept. 1999, *Zika 14325* (WTU); Kitsap Co., woods, near New Brooklyn Rd., Bainbridge Is., Puget Sound, elev. <100 m, T25N R2E S21, 28 Sept. 1999, *Zika 14425* (OSC, WTU); Pacific Co., roadside, Jacobson Rd, Heather, elev. 5 m, T15N R11W S30, 1 Oct. 1999, *Zika 14443* (WTU).

Significance. First report for Washington as a garden escape.

GLYCERIA CANADENSIS (Michx.) Trin. (POACEAE).— Grays Harbor Co., cranberry fields and ditches, with *Juncus effusus,* Evergreen Park Rd., elev. 5 m, T15N R11W S7, 29 Sept. 1998, *Zika 13646* (WTU); Pacific Co., ditches with *Leersia oryzoides,* Jim Street, 4 km N of Ilwaco, elev. 5 m, T10N R11W S22, 12 Sept. 1998, *Zika 13591* (WTU); ditches, N of Black Lake, elev. 5 m, T10N R11W S28, 29 Sept. 1998, *Zika 13636* (WTU).

Previous knowledge. Native to eastern North America, west to Minnesota. Collected in "a cranberry marsh" in adjacent Clatsop Co., Oregon in 1929 (*Henderson 11841* ORE), 30 km SE, where in 1999 it was a well established weed. Rattlesnake grass is also recorded as a rare weed in southern British Columbia.

Significance. First collection for Washington.

HELLEBORUS FOETIDUS L. (RANUNCULACEAE).—San Juan Co., common in meadow with *Festuca arundinacea, Pteridium, Rubus armeniacus,* near False Bay, San Juan Is., Puget Sound, elev. 20 m, T34N R3W S4, 30 May 1999, *Zika 13766* (WTU).

Previous knowledge. Stinking hellebore is an ornamental native to Europe, planted west of the Cascade Mtns. in the Pacific Northwest.

Significance. First record as an garden escape in Washington.

HYPERICUM BOREALE (Britton) E. Bickn. (Clusiaceae).—Grays Harbor Co., cranberry fields and drainage ditches, Evergreen Park Rd., elev. 5 m, T15N R11W S7, 29 Sept. 1998, *Zika 13640* (WTU); bulldozed field, near Hogan Rd., North Bay, elev. 3 m, T18N R11W S17, 4 Oct. 1999, *Zika 14484* (WTU); Pacific Co., sandy banks near cranberry fields, Pioneer Rd., elev. 5 m, T10N R11W S10, 12 Sept. 1998, *Zika 13594* (WTU); swale between sand dunes, marine beach near 10th St., Long Beach, elev. 2 m, T10N R11W S17, 1 Oct. 1999, *Zika 14446* (WTU).

Previous knowledge. Native to eastern North America, as far west as Minnesota. Northern St. Johnswort is a weed associated with cranberry agriculture on the Oregon coast in Coos and Curry Cos., 300 km to the south.

Significance. First record for Washington.

HYPERICUM CANADENSE L. (CLUSIACEAE).—Grays Harbor Co., cranberry fields and drainage ditches, with *Juncus effusus,* Evergreen Park Rd. elev. 5 m, T15N R11W S7, 16 Sept. 1999, *Zika 14348 & Weinmann* (WTU); ditch, Burrow Rd., N Bay, elev. 3 m, T18N, R11W S17, 4 Oct. 1999, *Zika 14483* (WTU); Pacific Co., sandy cranberry field, near Pioneer Rd., elev. 5 m, T10N R11W S9, 30 Sept. 1999, *Zika 14433* (WTU); ditches between cranberry fields, with *Hypericum anagalloides,* 1 km E of Long Lake, elev. 6 m, T15N R11W S17, 19 Oct. 1998, *Zika 13667* (WTU).

Previous knowledge. Canada St. Johnswort is native to eastern North America as far west as Manitoba, and adventive on cranberry farms on the Oregon coast in Coos and Curry Cos., 300 km to the south.

Significance. First record for Washington.

HYPERICUM ELLIPTICUM Hook. (Clusiaceae).—Grays Harbor Co., cranberry field, with *Equisetum arvense,* Cranberry Rd., Grayland, elev. 5 m, T15N R11W S6, 16 Sept. 1999, *Zika 14342* (UC, WS, WTU); Pacific Co., moist sandy ground, cranberry field, with *Oenanthe,* Heather Rd., Heather, elev. 5 m, T15N R11W S20, 16 Sept. 1999, *Zika 14353* (OSC, US, WTU).

Previous knowledge. Pale St. Johnswort is native to eastern North America, west to North Dakota.

Significance. First report for Washington.

HYPERICUM MUTILUM L. (CLUSIACEAE).—King Co., shores of Phantom Lake, with *Scutellaria lateriflora, Lysimachia thyrsiflora, Juncus balticus,* Bellevue, elev. 75 m, T24N R5E S2, 15 Oct. 1999, *Zika 14605 & Weinmann* (WTU); Skagit Co., wet bank, with *Typha latifolia, Myosotis laxa, Potentilla palustris,* Gandy Lake outlet creek, 5 km NW of Concrete, elev. ca. 245 m, T36N R8E S32, 1 Aug. 1989, *Naas 5536* (WTU); Gandy Lake, opening in cattail marsh, elev. ca. 250 m, 24 Aug. 1973, *Naas & Cheney 2751* (WTU).

Previous knowledge. Native to eastern North America as far west as Oklahoma. Dwarf St. Johnswort is recorded as a weed at low elevations 900 km to the south, in Butte and Glenn Cos., California. Skagit Co. records were previously identified as *H. majus.*

Significance. First report for Washington.

JUNCUS CANADENSIS J. Gay ex Laharpe (Juncaceae).—Clallam Co., Ericsons Bay, Lake Ozette, elev. 10 m, T30N R15W S8, 3 Aug. 1986, *Buckingham et al. 3787, & Ceska 20607* (ONP) [herbarium of Olympic National Park]; Grays Harbor Co., cranberry fields, with *Vaccinium macrocarpon,* 1 km SE of Horseshoe Lake, elev. 5 m, T15N

R11W S6, 19 Oct. 1998, *Zika 13658* (WTU); damp bulldozed ground, with *Juncus supiniformis,* near Burrow Rd., North Bay, elev. 3 m, T18N R11W S17, 4 Oct 1999, *Zika 14486* (WTU); Pacific Co., ditch near cranberry fields, with *Glyceria canadensis,* Jim Street, elev. 5 m, T10N R11W S22 W1/2, 12 Sept. 1998, *Zika 13588* (WTU); cranberry fields, with *Potentilla pacifica,* 0.8 km E of Long Lake, elev. 5 m, T15N R11W S17, 19 Oct. 1998, *Zika 13670* (WTU); Skagit Co., *Sphagnum* mat, shore of Summer Lake, with *Sarracenia purpurea, Eriophorum virginicum, Vaccinium oxycoccus,* elev. 200 m, T33N R5E S21, 27 Sept. 1999, *Zika 14419, Weinmann & Weinmann* (MICH, WTU); small pond ca. 0.2 km N of Summer Lake, elev. 200 m, 27 Sept. 1999, *Zika 14423, Weinmann & Weinmann* (WTU).

Previous knowledge. Native to eastern North America, west to Minnesota. Canada rush is known as a weed in wetlands and in cranberry fields in British Columbia and in Coos and Curry Cos., Oregon. Recent reports of *J. brevicaudatus* from Washington (Buckingham *et al.,* Flora of the Olympic Peninsula, 1995) are based on collections of *J. canadensis.*

Significance. First documented report for Washington.

JUNCUS DIFFUSISSIMUS Buckley (JUNCACEAE).—Cowlitz Co., moist sand flats, Cowlitz R., with *Phalaris arundinacea, Salix sitchensis,* Longview, elev. 2 m, T7N R2W S11, 26 Sept. 1998, *Zika 13624* (WTU); sandy shoreline, Cowlitz R., N end of Castle Rock, 18 July 1994, *Kollock & Wilson s.n.* (OSC, WTU); moist gray sand, Toutle R., with *Juncus bolanderi,* 5 km N of Castle Rock, elev. 24 m, T10N R2W S27, 15 Sept. 1998, *Zika 13614* (WTU); cobble shore, S Fork Toutle R., 1.8 air km E of Toutle, elev. 137 m, T10N R1E S29, 20 Oct. 1998, *Zika 13671* (WTU).

Previous knowledge. Native to the eastern United States, west to Kansas. Known as a weed in Sacramento Valley of California, 800 km to the south. Discovered in the Castle Rock area by Loverna Wilson and Kathleen Kollock in 1994.

Significance. First report for Washington. *Juncus diffusissimus* successfully colonized riverine sand and ash deposits from the 1980 eruption of Mt. St. Helens. Slimpod rush is now frequent on volcanic debris from the mouth of the Cowlitz R. upriver to the shores of S Fork Toutle R. However, the linear population continues upstream of the ash deposits. This distribution suggests the population was originally introduced on private logging lands on the upper tributaries of S Fork Toutle R. At present *J. diffusissimus* is absent from suitable habitat on other tributaries in the Cowlitz R. basin.

JUNCUS PELOCARPUS E. Meyer (Juncaceae).—Grays Harbor Co., cranberry fields, Blake Rd., Grayland, elev. 5 m, T15N R11W S6, 19 Oct. 1998, *Zika 13659* (WTU), disturbed damp sandy ground, near Hogan Rd., N shore of N Bay, elev. 3 m, T18N R11W S17, 4 Oct. 1999, *Zika 14508* (WTU); Pacific Co., moist sandy ground, near irrigation pond, Cranberry Rd., elev. 5 m, T11N R11W S34, 12 Sept. 1998, *Zika 13597* (WTU); ditches and cranberry fields, 0.8 km E of Long Lake, elev. 6 m, T15N R11W S17, 19 Oct. 1998, *Zika 13669* (WTU).

Previous knowledge. Native to eastern North America, as far west as Minnesota. Brown-fruited rush was first recorded in 1958 as a cranberry weed in Coos Co., OR, 300 km to the south.

Significance. The first report for Washington.

LONICERA PILEATA Oliv. (CAPRIFOLIACEAE).—Clal-

lam Co., E end of Lake Crescent, bird-sown shrubs scattered in forest and at edge of clearings, with *Tsuga heterophylla, Alnus rubra,* elev. 195 m, T30N R9W S28, 22 Nov. 1997, *Zika 13408* (WTU).

Previous knowledge. Box-leaved honeysuckle is native to China and commonly planted west of the Cascades.

Significance. First report as a garden escape in Washington.

SALIX PURPUREA L. (SALICACEAE).—Wahkiakum Co., mouth of Elochoman R., N shore, scattered on sand spit, with *S. sessilifolia,* elev. 3 m, T9N R6E S28, 4 June 1999, *Zika 13779* (CAN, WTU).

Previous knowledge. Basket willow is native to Eurasia, and occasionally planted by weavers. It is weedy in eastern North America, W to Colorado.

Significance. First report as a wild plant in Washington.

TRIADENUM FRASERI (Spach) Gleason (CLUSIACEAE).—Pacific Co., cultivated cranberry field, 1 km N of Black Lake, elev. 5 m, T10N R11W S28, 31 Aug. 1999, *Zika 14176* (US, WTU); sandy cranberry field, S of Gile Lake, elev. 5 m, T10N R11W S3, 30 Sept. 1999, *Zika 14438* (WTU).

Previous knowledge. Native to eastern North America, W to Saskatchewan. Marsh St. Johnswort was first detected as a weed in cranberry farms of British Columbia in 1913 (F. Lomer, pers. comm.), where it has been reported as *T. virginicum* (Hueppelsheuser & Emery, A Field Guide to Common Weeds of Cranberries in British Columbia, 1996).

Significance. First report for Washington.

VACCINIUM CORYMBOSUM L. (Ericaceae).—Grays Harbor Co., cranberry fields near Hogan Rd., N shore of North Bay, elev. 3 m, T18N R11W S17, 4 Oct. 1999, *Zika 14502* (WTU); King Co., boggy N shore of Panther Lake, 6 km S of Renton, elev. 75 m, T22N R5E S5, 15 Oct. 1999, *Zika 14610 & Weinmann* (WTU); undisturbed boggy shore of Tub Lake, 140th St., Burien, elev. 100 m, T23N R4E S16, 14 Oct. 1999, *Zika 14596 & Jacobson* (WTU); common escape near large cultivated blueberry fields, Mercer Slough, Bellevue, elev. 5 m, T24N R5E S5, 6 Oct. 1999, *Zika 14553 & Weinmann* (WTU); marshy NW shoreline of Union Bay, Seattle, elev. 4 m, T25N R4E S16, 27 Aug. 1999, *Zika 14143 & Jacobson* (WTU).

Previous knowledge. Highbush blueberry is commonly cultivated for fruit west of the Cascades. It is native to eastern North America, west to Texas. Birds disperse the seed.

Significance. First report for Washington as an escape from cultivation.

VACCINIUM MACROCARPON Ait. (Ericaceae).—Grays Harbor Co., roadside ditch, with *Anthoxanthum, Rubus spectabilis,* Route 105, 2.5 km E of Ocosta, elev. 15 m, T16N R11W S11, 16 Sept. 1999, *Zika 14340* (WTU); Pacific Co., peaty clearing, near Jim St., 2 km NE of Seaview, elev. 5 m, T10N R11W S22, 31 Aug. 1999, *Zika 14195* (WTU).

Previous knowledge. Cranberry is native to eastern North America, west to Minnesota. First introduced as a crop plant in Oregon in 1885, and known as a local weed in California and British Columbia. Reported as questionably escaped in Washington (Buckingham et al. Flora of the Olympic Peninsula, 1995).

Significance. First documentation as a naturalized species in Washington.

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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

SPECIAL ISSUE
THE JEPSON HERBARIUM 50TH ANNIVERSARY CELEBRATION AND SCIENTIFIC SYMPOSIUM:
DISCOVERY, COMMUNICATION, AND CONSERVATION OF
PLANT BIODIVERSITY IN CALIFORNIA—JUNE 16–18, 2000

CONTENTS

THE JEPSON HERBARIUM 50TH ANNIVERSARY CELEBRATION AND SCIENTIFIC SYMPOSIUM:

DISCOVERY, COMMUNICATION, AND CONSERVATION OF PLANT BIODIVERSITY IN CALIFORNIA
JUNE 16–18, 2000

This warm weekend in June witnessed an incredible outpouring of energy, information, science, love of plants, and just plain fun, revolving around the golden anniversary of the founding of the Jepson Herbarium. More than 210 registrants converged on the Valley Life Sciences Building, UC Berkeley, for a diverse array of activities. On Friday afternoon, many visitors from out of town toured the facilities, worked in the herbarium collection, and enjoyed a formal reception that lasted well into the evening. In addition, participants from around and outside of California met that afternoon to discuss innovative ways to pursue floristic projects in western North America. A primary focus of this special networking and brainstorming session was the potential development of electronic approaches to floristics within a collaborative framework, taking advantage of shared resources and joint funding opportunities.

Saturday morning was devoted to a plenary session that set the stage for the main issues to be examined the rest of the day. Beginning this session, Barbara Ertter spoke on the need for basic surveys of biodiversity, to the extent that even in a relatively well studied state like California a dozen new species are discovered and described each year. Bruce Baldwin followed with several test cases from the California flora showing how knowledge of phylogenetic relationships of plants is essential to determining their proper classification, even at the species level; evolutionarily significant, yet often cryptic, biodiversity is everywhere. Theodore Barkley (Botanical Research Institute of Texas) summarized the need for informatics tools to make the huge amount of data on biodiversity available to the broad array of "consumers" of biodiversity information, and Ken Berg (U.S. Fish & Wildlife Service) presented a convincing case for us to get out in the trenches immediately and do what we can to protect plant biodiversity in this rapidly developing part of the world. Finally, Brent Mishler discussed the need for integrated studies of the California flora linking practical floristics and conservation biology with academic systematics, a subject at the heart of the scientific goals of the weekend.

On Saturday afternoon two sets of concurrent sessions (three sessions per set), allowed the participants to break out into smaller groups, thereby fostering discussion and interchange on the basic subjects of the morning talks. We encouraged folks to go to sessions that were on subjects somewhat outside their normal interests. Judging by the debates, interesting questions, and sharing of information in the halls afterward, it was a great success!

Following a break for further tours of the Herbaria, we re-convened at the Radisson Hotel at the Berkeley Marina for a reception and the gala 50th Anniversary Celebration Banquet, with Jepson Trustee Chair Roderic Park as the Master of Ceremonies. After a truly sumptuous meal, Richard Beidleman gave an entertaining tribute to Willis Linn Jepson, with many wonderful photographs and anecdotes from his extensive biographical research. Bob Ornduff followed with equally entertaining views of several other historical figures in California botany, noting how their careers and interests interacted with Jepson's. One of the many treats of the evening was the presence of two of Jepson's great nieces—Mrs. Margaret Van Eck and Mrs. Louise Condeff, as well as two of his former graduate students, Dr. Lincoln Constance and Dr. Mary Bowerman, and relatives of a third, Mrs. Virginia Bailey.

Sunday was devoted to a fine set of field trips led by expert botanists to some of the places Jepson and his students loved. There were packed trips to Point Reyes, Mount Diablo, Santa Cruz sandhills, Redwood Regional Park, and Solano County, with topics ranging from bryophytes to restoration to endangered species. Despite all the important indoor scientific activities, deep down it is being out in the field with the plants that excites us most of all.

We all know who Willis Linn Jepson was as a botanist, in part because of the fine articles by Richard Beidleman in the Jepson Globe and this issue of *Madroño,* and the paper by Lincoln Constance in an earlier issue of *Madroño* (1995, volume 42, number 2). But, what we were celebrating this weekend was Jepson as an institution-builder. Despite his reputation as a somewhat cantankerous individualist, he had the foresight to envision the need for a permanent botanical institution devoted to the flora of California at one of the premier universities in the state. He followed up this vision with a gift in his will, which in 1950 established the Jepson Herbarium. We owe the central position and guaranteed continuance that the University and Jepson Herbaria now hold at UC Berkeley largely to Jepson's foresight. The association of the Jepson Herbarium with a world-class university is unique in the state, and nearly unique across the US. This

gives us a tremendous opportunity to interface traditional approaches to plant systematics and conservation with the most up-to-date scientific advances, to the benefit of general research, formal university education, and public outreach.

Since the herbarium was established in 1950, other creative, hard working people have devoted their lives and fortunes to the Jepson Herbarium. Rimo Bacigalupi, the first Jepson Curator, left his published work and collections, as well as an endowment fund which is used to enhance research and publication in the Herbarium. The second Jepson Curator, Larry Heckard, likewise left a distinguished body of work and created an endowment fund that provides grants to UC Berkeley botanists for a spectrum of studies. From the Curators on down, many generous people have enhanced the Herbarium over its history through their continued support, and it is the totality of these efforts that we recognized with this weekend-long celebration. We would in particular like to thank the many staff members, students, and associates who helped make possible the weekend celebration and this special issue of *Madroño*—especially Betsy Ringrose who was involved in all aspects of the organization.

Inclusion of the proceedings of the Jepson Herbarium's 50th Anniversary Celebration in the volume of *Madroño* dedicated to the late Robert Ornduff is particularly fitting given Bob's long history of involvement with the Jepson Herbarium. In addition to a full biography of Dr. Ornduff, who died only months after giving his post-banquet talk, the proceedings consist of the morning plenary session talks, several afternoon presentations that complemented the other papers particularly well, Richard Beidleman's post-banquet biography of Willis Linn Jepson, and a previously unpublished manuscript by Jepson himself that seemed exceptionally appropriate. Ken Berg was unfortunately unable to provide a written version of his excellent talk ("Conserving California's Flora: Who Will Answer the Call?") due to career developments. Dr. Ornduff's post-banquet talk, "Piss and Vinegar: Skeletons in our Botanical Closet," was geared more to the lay audience and accordingly was published in *Fremontia* (volume 28, pages 18-20).

—Brent D. Mishler, Barbara Ertter, Bruce G. Baldwin, and Staci Markos, Jepson Herbarium, 1001 VLSB #2465, University of California, Berkeley, CA 94720.

ROLES FOR MODERN PLANT SYSTEMATICS IN DISCOVERY AND CONSERVATION OF FINE-SCALE BIODIVERSITY

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Abstract

Systematic methods involving the use of DNA data and genealogical analysis have been widely applied to higher-level phylogenetic questions in plants but much less commonly to discovering plant lineages corresponding to minimal-rank taxa (i.e., species, subspecies, and varieties) or to refining plant classification at the finest levels. Recent research in the Jepson Herbarium integrating extensive field sampling, biosystematic data, and molecular phylogenetics provides examples from the California flora for assessing the value of modern systematic approaches as a means of discovering fine-scale plant diversity. Results have sometimes led to taxonomic changes at the levels most important for biodiversity assessment and have allowed resolution of systematic questions important to establishing conservation strategies. Angiosperm groups newly resolved with molecular data include both morphologically distinctive and morphologically cryptic lineages that have been previously treated within more broadly circumscribed species, subspecies, or varieties. Taxonomic recognition of such newly resolved lineages is often necessary if taxonomy is to reflect monophyletic groups and fine-scale units of biodiversity. To promote discovery, recognition, and conservation of plant lineages, systematists are advised to sample widely within minimal-rank taxa (including rare taxa) in the field and in herbaria, to consider previous taxonomies, to voucher all collections, to examine multiple lines of systematic evidence, and to publish taxonomic changes, including nomenclatural changes. Scientists involved in biodiversity management and conservation are advised to regard circumscriptions of all taxa as hypotheses of natural groups, to recognize that those hypotheses are subject to change, and to welcome taxonomic and nomenclatural changes that reflect an improved understanding of natural groups. Conservation biologists are urged to bear in mind that species or infraspecific taxa are not necessarily the minimal units of biodiversity. To conserve evolutionary lineages (and potential for future evolution), plant managers must seek to conserve representative populations of taxa from throughout their geographical and ecological distributions, must resist indiscriminate use of non-local germplasm in restoration efforts, and must consider cryptic biodiversity in regional conservation planning.

Systematics is fundamental to understanding of biodiversity. The most widely recognized organismal units of biodiversity, i.e., species, may not represent natural evolutionary groups or may not reflect the finest-scale natural groups that can be resolved and described by systematists. Modern systematic approaches that allow a genealogical perspective on biodiversity hold great promise as a means of achieving a refined taxonomy that better reflects evolutionary lineages of organisms throughout the tree of life (e.g., Angiosperm Phylogeny Group 1998). To date, modern systematic approaches to resolving evolutionary relationships have been applied by plant systematists mostly to questions concerning groups of recognized species or higher-level taxa (see Soltis et al. 1998). Recent studies of higher-level plant phylogeny have yielded insights into broad-scale evolutionary and biogeographic patterns that are directly relevant to biodiversity assessment and prioritization of conservation efforts (e.g., Vane-Wright et al. 1991; Mishler 1995; Faith 1996; reviewed by Soltis and Gitzendanner 1998).

Modern systematic methods have been applied less commonly to testing the naturalness of minimal-rank taxa (i.e., species, subspecies, and varieties), which are of most immediate concern to conservation biologists, ecologists, and floristicians (e.g., Rieseberg et al. 1988; see Soltis et al. 1992). Studies of phylogeographic diversity—fine-scale, geographically structured evolutionary lineages corresponding to "Evolutionarily Significant Units" (*sensu* Moritz 1994)—also have been extremely limited for plants (e.g., Fujii 1997; Soltis et al. 1997; Olsen and Schaal 1999; Tremblay and Schoen 1999; Shaw 2000; also see Schaal et al. 1998; Schaal and Olsen 2000), especially by comparison with the rich literature on animal phylogeography (reviewed by Avise 2000). As noted by Moritz (1995, 1999) and Coates (2000), conserving independently evolving sets of populations not only preserves biodiversity but also may be the best strategy for conserving the potential for future evolution. On a regional scale, refined understanding of phylogeographic patterns across organismal groups may allow for improved resolution of biodiversity hot-spots and identification of critical areas for conservation attention (see Moritz and Faith 1998).

In this paper, I present examples of previously

undetected diversity resolved from studies of the California flora conducted in the Jepson Herbarium. These studies illustrate both the potential and the proven value of applying modern systematic methods to discovery of fine-scale plant diversity and to refining classifications of minimal-rank plant taxa. Finally, I make general recommendations for how systematists and other biodiversity scientists and planners may promote discovery and conservation of plant diversity.

EXPLORATION IN THE FIELD AND LABORATORY

Well-focused field exploration (see Ertter 2000a) and detailed systematic analysis are complementary components of an effective strategy for discovering plant diversity. As reviewed by Ertter (2000b), botanical field exploration in western North America, often by non-academic professionals and amateurs, has been a continuing source of floristic novelties. Modern systematic approaches can contribute greatly to the process of discovery by offering a rigorous means of resolving the systematic status of recently discovered plant populations. For example, DNA sequence variation may clarify whether phenotypically unusual populations or sets of populations belong within previously described, minimal-rank taxa or represent undescribed evolutionary groups (e.g., Baldwin 1999a). Data from DNA also may allow confident taxonomic placement of newly discovered plants that are evidently distinct from any described minimal-rank taxon but of uncertain position (e.g., Boyd and Ross 1997). Conversely, fine-scale systematic studies depend on extensive field sampling across the geographical and ecological distribution of taxa for assessing naturalness of groups and detecting any unrecognized diversity within a group. Phylogeographic studies have demonstrated the potential for discovery of geographically distinct, and often morphologically cryptic, evolutionary lineages within both widespread and narrowly distributed species (see Soltis et al. 1997; Moritz 1999; Avise 2000; Riddle et al. 2000). Systematic studies and floristic surveys that involve extensive geographic sampling of widespread taxa as well as locally restricted taxa are therefore advisable to maximize the potential for discovering unrecognized plant diversity.

The prospect for floristic discoveries to result from more detailed systematic analyses of western North American plant groups appears great. Young lineages, which account for much of the endemic plant diversity in western North America, e.g., California (Raven and Axelrod 1978), can be expected to exhibit mosaic or cryptic phenotypic variation from minimal divergence, differential sorting of ancestral polymorphism through descendant lineages (see Maddison 1995), or hybridization (see Arnold 1997). Climatic and geologic upheaval and extensive species turnover seen in the plant fossil record during the mid to late Cenozoic in western North America has been associated with the rise of diverse lineages of annuals and perennials that are largely or entirely restricted to the region (Axelrod 1992; Graham 1999). The high degree of endemism, ca. 50% of species, in the California Floristic Province, i.e., the Mediterranean-climatic region of western North America (Raven and Axelrod 1978), largely reflects high diversity in neoendemic groups wherein often only minimal morphological divergence has occurred between evolutionary lineages.

Systematists in California and elsewhere in western North America have long appreciated the complexity of the regional flora and the need for in-depth evolutionary investigations to reveal natural units of biodiversity. The San Francisco Bay Area botanists Harvey Monroe Hall, Ernest Babcock, G. Ledyard Stebbins, Jens Clausen, David Keck, William Hiesey, and others pioneered the incorporation of genetic principles and experimental approaches into systematics in a highly successful effort to resolve evolutionary lineages and understand complex patterns of variation in the California flora (e.g., Babcock and Hall 1924; Stebbins 1950; Clausen 1951; also see Smocovitis 1997). Subsequent developments in systematics now allow even more progress in discriminating natural plant groups and refining the taxonomy of western North American plants.

Advances in phylogenetic theory and methodology, together with the development of accessible high-speed computers, now permit simultaneous analysis of large numbers of variable characters to produce rigorous hypotheses of evolutionary relationships within plant groups, as well as estimates of support for resolved lineages (see Swofford et al. 1996). Character changes (resulting from mutations) allow diagnosis of monophyletic groups (=evolutionary lineages or clades), the most natural groups recognized by systematists (Hennig 1966; see Mishler 1995, 2000a, b)—plants belonging to monophyletic groups are more closely related to one another than to plants in other groups. Access to an ever-increasing number of macromolecular characters from DNA sequences has enhanced the prospects for systematists to attain fine-grained, robust resolution of evolutionary lineages (see Hillis et al. 1996; Soltis et al. 1998).

EXAMPLES OF RECENT PLANT DISCOVERIES FROM SYSTEMATIC STUDIES

To illustrate the utility of modern systematic methods for discovery of plant groups, I present below some examples from research conducted in my lab at the Jepson Herbarium, principally on Californian angiosperm lineages. Although categorization of the examples is somewhat artificial, three general types of problems are addressed: confusing variation within taxa, resolution of cryptic biodiversity, and questionably distinct rare taxa.

I. *Variation within taxa reexamined.* The first category of examples comprises groups wherein morphological variation within a taxon was of uncertain systematic significance until phylogenetic studies were undertaken.

Deinandra bacigalupii: A narrow endemic misplaced in a widespread species.—*Deinandra* is a species-rich genus of tarweeds (Madiinae, Compositae) reinstated for members of *Hemizonia sensu* Keck (1959) that are most closely related to *Holocarpha* (Baldwin 1999b). Until 1999, an ca. 8-rayed *Deinandra* from alkaline meadows in the Livermore Valley, California, was treated within *D.* [*Hemizonia*] *increscens* subsp. *increscens,* a mostly coastal taxon known otherwise from Santa Barbara County to Monterey County, California (Tanowitz 1982), more than 75 km south of Livermore Valley. Morphologically, the Livermore Valley tarweed is highly similar to *D. increscens* except in anther color and pappus characteristics. Robert F. Hoover collected and left unidentified to species the Livermore Valley tarweed as early as 1966. Rimo Bacigalupi annotated the UC accession of the first known collection (by Hoover) as not matching any published species of *Hemizonia.*

Dean Kelch and Robert Preston independently collected the Livermore Valley tarweed in the 1990's and brought specimens to me with concerns that the plant was not identifiable with *The Jepson Manual: Higher Plants of California* (Hickman 1993). The characteristics of yellow to brownish, rather than "black" (i.e., dark purple), anthers in the Livermore Valley plants was in conflict with placement in *Deinandra* [*Hemizonia*] *increscens* and ray laminae of the plants were much too short for *D.* [*Hemizonia*] *pallida.* Further examination of the plants in comparison with other deinandras revealed that the pappus was much shorter and more irregular than in other populations then assigned to *D. increscens* (Baldwin 1999a). Chromosome counts of the Livermore Valley tarweed of $2n = 12$ II, the modal chromosome number in *Deinandra* (as in *D. increscens*), were inconclusive about relationships of the plants (Baldwin 1999a).

Results of phylogenetic analysis of nuclear ribosomal DNA (rDNA) sequence data, in concert with the morphological evidence, led me to conclude that the Livermore Valley tarweed is not a member of *Deinandra increscens* or any other previously recognized species of *Deinandra* (Fig. 1; Baldwin 1999a). Representatives of the two most divergent groups of *D. increscens,* i.e., *D. i.* subsp. *increscens* and *D. i.* subsp. *villosa,* were resolved as a well-supported monophyletic group to the exclusion of representatives of the other six recognized species of the "northern lineage" of *Deinandra* and the Livermore Valley tarweed. The Livermore Valley tarweed does not appear to be of recent hybrid origin based on 10 unambiguous rDNA mutations not shared with any other sampled
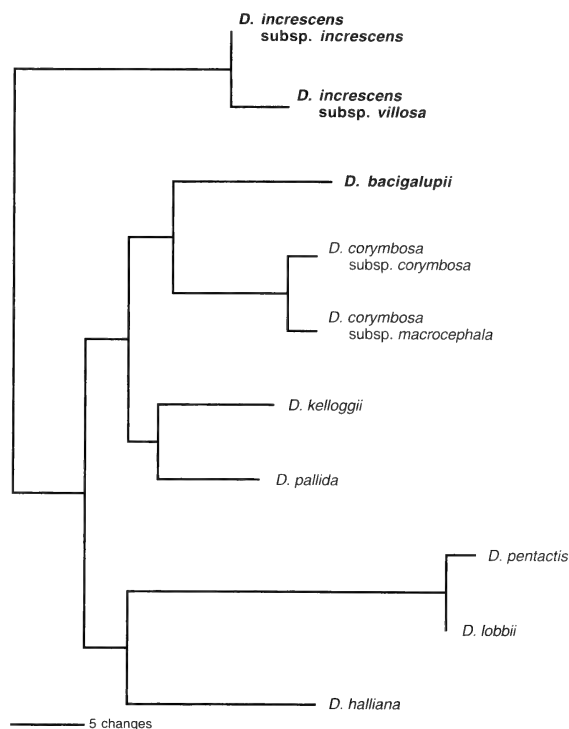
FIG. 1.   The most parsimonious tree from phylogenetic analysis of 18S-26S nuclear ribosomal DNA sequences of the external and internal transcribed spacers for the northern lineage of *Deinandra* (Compositae—Madiinae; Baldwin unpublished data). The outgroup (*D. minthornii*) used for rooting the tree is not shown, nor are tree statistics and support values (to be published elsewhere). Note the extensive divergence of the Livermore Valley tarweed (*D. bacigalupii*) from other representatives of *Deinandra* and the remote phylogenetic position of *D. bacigalupii* from *D. increscens,* the species in which the Livermore Valley tarweed was earlier treated.

plants from the "northern lineage" of *Deinandra* (Baldwin, unpublished data).

Evidence from DNA substantially augmented morphological evidence for distinctiveness of the Livermore Valley tarweed from *D. increscens.* Recognition of *D. bacigalupii* as distinct from *D. increscens* improves our understanding of diversity in *Deinandra* and rare plants in general in the Springtown wetlands area near Livermore, California. *Deinandra bacigalupii* has been regarded as an example of a plant species that was discovered "in front of the bulldozer" (Ertter 2000b), i.e., that came close to being driven to extinction prior to being recognized as distinct.

Layia gaillardioides: Interpopulational variation of phylogenetic significance.—*Layia gaillardioides,* the woodland layia, has been regarded as an example of a species displaying substantial morphological variation among populations (Clausen 1951). Ray laminae may be uniformly deep yellow or have white, greenish, or pale yellow apices de-
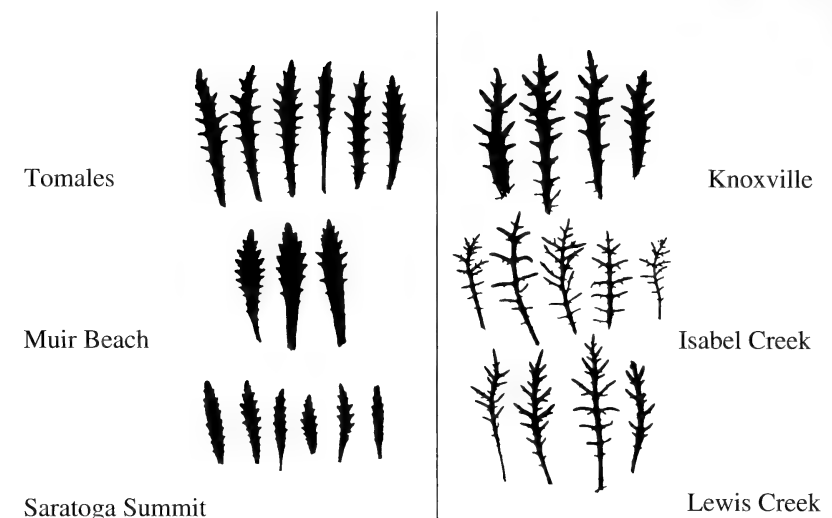
Fig. 2. Basal leaf variation in the woodland layia, *Layia gaillardioides* (modified from Clausen 1951). Leaves separated by the vertical line correspond to outer (left) and inner (right) Coast Range populations in central and northern California. The populational differences shown here correspond to variation across three divergent molecular lineages that do not appear to constitute a natural group (Baldwin, unpublished data).

pending on the population examined. Clausen (1951) noted that inner and outer Coast Range populations differ in stem thickness and degree of lobing of the basal leaves, characteristics that he concluded were heritable and ecologically significant (Fig. 2).

Phylogenetic analysis of *Layia* has revealed evidence that *L. gaillardioides* as circumscribed at present represents an unnatural group (Baldwin, unpublished data). Populations shown earlier by Clausen to be morphologically distinct constitute three distinct lineages that apparently are not most closely related to one another. Two lineages of *L. gaillardioides* are more closely related to *L. carnosa, L. hieracioides*, and *L. septentrionalis* than to a third lineage of *L. gaillardioides*. Each of the groups resolved within *L. gaillardioides* is well-supported by unique rDNA mutations, and relationships among the lineages and related species are likewise robust based on rDNA data. Evolutionary lineages within the woodland layia conform to a typical phylogeographic pattern except that the natural groups within *L. gaillardioides* do not constitute a clade and instead represent a paraphyletic or (conceivably) polyphyletic group (see Riddle et al. 2000 for similar examples). Recognition that *L. gaillardioides* has been circumscribed too broadly and comprises multiple natural groups, each probably warranting taxonomic distinction, may be an important conservation concern given the evidently scattered distribution and small size of woodland layia populations. Sampling of additional populations and DNA regions is now underway to resolve the precise delimitation of each evolutionary lineage within *L. gaillardioides* s. lat. prior to describing segregate taxa.

Lessingia: Problems in species and varietal circumscriptions in the "yellow group."—Systematic investigations by Markos (2000; also see Markos and Baldwin 2001) revealed an outstanding example of misinterpreted morphological variation in another lineage of annuals in the California Compositae, namely, in the "yellow group" of *Lessingia* (Astereae). Markos (2000) found that annuals in *Lessingia* constitute two major lineages that differ in disc corolla coloration—a pink-to-white-flowered lineage and a yellow-flowered lineage. Within the "yellow group," Markos (2000) used morphological and molecular data to resolve three major natural groups that span the boundaries of widely recognized species and varieties.

Markos (2000) found that different representatives of each of three taxa (*Lessingia gladulifera, L. glandulifera* var. *glandulifera,* and *L. lemmonii*) belong to different major lineages within the "yellow group." Morphologically, differences in shape of the style-branch appendages and presence or absence of a maroon band in the corolla throat diagnose the three primary lineages of yellow-flowered lessingias. Markos (2000) concluded from her phylogenetic data that the accepted taxonomy of *Lessingia* underrepresents the actual biodiversity of the group and warrants substantial revision (S. Markos, in prep.).

II. *Cryptic biodiversity.* Modern systematic methods have promising potential for allowing discovery of natural plant groups that are morphologically indistinguishable (or nearly so) from one another but may be geographically or ecologically distinct. As noted above, lineage diversity across the geographic distribution of a morphological or

biological species, i.e., phylogeographic diversity, has been widely reported in vertebrates but has not been extensively studied in plants (see Soltis et al. 1997; Avise 2000; Schaal and Olsen 2000). In Californian groups of annuals, members of my lab have found various examples of cryptic diversity associated with geography. Two examples are particularly important for illustrating groups that are not only morphologically cryptic but, based on multiple lines of evidence, must be recognized as distinct taxa because the well-supported but morphologically indistinct lineages are evidently not most closely related to one another.

Downingia yina.—Schultheis (2000) examined relationships throughout *Downingia* (Lobeliaceae) with special attention to a lineage corresponding to three morphological species: *D. bacigalupii*, *D. elegans* and *D. yina.* Earlier work by Weiler (1962) and Foster (1972) established that *D. yina* is cytologically highly unusual, with a broad dysploid series of chromosome numbers, i.e., $2n = 6, 8, 10,$ and 12 II. Chromosome "races" of *D. yina* are mostly geographically distinct but could not be distinguished reliably on the basis of morphology using multivariate analyses and other approaches (Schultheis 2000).

Schultheis (2000) extensively sampled *D. bacigalupii*, *D. elegans,* and *D. yina* throughout their geographic ranges in an attempt to discern the evolutionary significance of chromosomal variation in the group. She found strong phylogenetic signals from sequences of both chloroplast DNA (cpDNA) and nuclear rDNA for three major lineages with cytological and geographic integrity that each include populations of *D. yina.* One lineage corresponds to populations west of the Cascade Range, all with chromosome numbers of $2n = 6, 8,$ or 10 II, i.e., *D. elegans* ($2n = 10$ II) and populations of *D. yina* with $2n = 6, 8,$ or 10 II. The second lineage corresponds to a pocket in the southern Cascade Range of Oregon wherein populations of *D. yina* with $2n = 10$ II are found. The third lineage corresponds to populations east of the Cascades, with $2n = 12$ II, i.e., *D. bacigalupii* and *D. yina.*

Schultheis (2000) concluded that the three well-supported evolutionary lineages in *D. yina* warrant taxonomic recognition despite being only cryptically distinct morphologically. Congruence between two lines of molecular data leave minimal doubt that *D. yina* represents an example of divergent evolutionary lineages that remained morphologically static while closely related lineages (corresponding to *D. bacigalupii* and *D. elegans*) underwent considerable morphological change. Differences among the three major groups of *D. yina* in geographic distribution and nuclear genomic arrangements conceivably extend to physiological differences of fundamental importance to survivorship in distinct ecological settings.

Lasthenia californica—The goldfield genus *Lasthenia* (Compositae) has been the subject of a re-

cent molecular phylogenetic study by Chan (2000), who sampled widely across populations of each taxon recognized by Ornduff (1966, 1993). Chan found strong evidence from cpDNA and nuclear rDNA sequences for morphologically cryptic lineages in *L. californica,* the most widespread species recognized by Ornduff (1993).

Chan's (2000) cpDNA and nuclear rDNA data led him to propose the hypothesis that one set of populations of *L. californica sensu* Ornduff (1993) is most closely related to the outer coastal, endemic Californian taxa *L. macrantha* subsp. *macrantha* and *L. m.* subsp. *bakeri.* Chan concluded that the three taxa constitute a well-supported group exclusive of the Pacific Northwest endemic *L. macrantha* subsp. *prisca* and other populations of *L. californica sensu* Ornduff (1993). Chan (2000) also found that the two lineages corresponding to *L. californica sensu* Ornduff (1993) have somewhat distinct (but overlapping) geographic distributions and minor pappus differences, although some individuals of both groups are epappose and cannot be reliably distinguished morphologically. *Lasthenia californica sensu* Ornduff (1993) appears to represent another example, parallel to *Downingia yina,* of lineages that do not constitute a natural group but have remained morphologically similar while related lineages have undergone substantial morphological change.

Taxonomic recognition of cryptic plant groups.—Morphologically indistinct evolutionary groups such as the two examples discussed above (within *Downingia yina* and *Lasthenia californica*) present a special challenge to plant systematists and the botanical community. Cryptically distinct lineages that together constitute a monophyletic group may or may not be viewed as warranting taxonomic recognition. In the interests of accurate biodiversity assessment (which typically relies on taxa as units), I suggest that cryptic groups that are: (1) well-supported by different lines of molecular or other evidence, and (2) geographically or ecologically distinct should be recognized as taxonomically distinct. Well-supported, cryptically-distinct groups that are not even most closely related to one another (e.g., groups in *D. yina* and in *L. californica*) leave systematists committed to natural classification with no choices other than to recognize the cryptic groups as taxonomically distinct or to treat all members of the minimal monophyletic group encompassing the cryptic lineages and the related group(s) as a minimal-rank taxon. I believe that the second option is undesirable because it under-represents biodiversity.

Practicality of classification is a concern for plant systematists and other botanists, especially for those faced with accurately identifying plant taxa with minimal time and resources. A system of classification that does not allow some plant taxa to be identified on the basis of macroscopic morphological characteristics alone generally has been resisted

by vascular plant systematists (but not bryologists or other botanists). Insofar as geography or habitat characteristics often aid identification of cryptic lineages, practical problems arising from giving formal taxonomic status to morphologically indistinguishable groups may be limited. Eventually, advances in DNA analysis and computer technology may trivialize the process of screening for diagnostic genetic markers, even in the field, thereby allowing botanists to be less reliant on morphological characteristics for plant identification. I recognize, however, that for plant groups wherein morphology has evolved even faster than DNA sequences in commonly examined, rapidly-evolving gene regions, e.g., in some examples of insular adaptive radiation (see Baldwin et al. 1998), morphology may provide a finer-scale perspective on evolutionary lineages than most easily obtained DNA data.

Strict adherence to a criterion of macroscopic diagnosability for all vascular plant taxa places unacceptable and unnatural limits on the information content of our taxonomy and potentially jeopardizes important segments of biodiversity because of a human bias toward recognizing only what can be seen with minimally-assisted human eyesight. From a biological standpoint, cryptic differences between plant groups, e.g., in characters associated with ecophysiology, can be more important to the integrity and fitness of plant groups than differences that humans can perceive visually. From a conservation perspective, taxonomic recognition of cryptically distinct natural groups may be important to ensure their legal protection (e.g., only formally-named plant lineages are eligible for protection under the U.S. Endangered Species Act). Taxonomic status for cryptic groups also may help to ensure their protection from misguided restoration efforts that result in combining germplasm from different evolutionary lineages treated within the same minimal-rank taxon, with consequent loss of lineage integrity and possible outbreeding depression (see Moritz 1999). From a more general perspective, adherence to the belief that plant systematics is a science that seeks to discern real entities of nature, i.e., evolutionary groups, dictates that plant taxonomy should reflect rigorous hypotheses of relationship rather than convenient but artificial or oversimplistic assemblages. Based on available evidence, I suspect that widespread recognition of cryptic taxa would result in only a modest refinement, not a major overhaul, of plant taxonomy.

III. *Conservation prioritization.* Mishler (1995) and others have discussed the potential value of phylogenetic data on the age and position of lineages for prioritizing conservation efforts (reviewed by Soltis and Gitzendanner 1998). On an even more fundamental level, modern systematic data can help to resolve whether rare taxa of questionable naturalness truly represent evolutionary lineages worthy of conservation attention and re-

sources. Skinner et al. (1995) identified over 150 examples of rare, minimal-rank taxa of Californian vascular plants that needed systematic attention. The two rare taxa discussed below are examples of groups that were studied systematically in part to determine whether they warrant continued recognition and, for *Blepharizonia,* to determine whether gene flow between species represents a conservation concern.

Blepharizonia plumosa: Rare species or minor morphological variant?—Baldwin et al. (2001) examined biosystematic and phylogenetic data for *Blepharizonia* to assess whether the common big tarweed, *B. plumosa* subsp. *viscida,* warrants taxonomic distinction from the rare big tarweed, *B. plumosa* subsp. *plumosa.* Keck (1959) regarded the two taxa as allopatric but recent field work by Robert Preston established that the two taxa are mosaically sympatric in the northern Mt. Hamilton Range, California, where Baldwin et al. (2001) sampled the big tarweeds for crossing and molecular studies. Phylogenetic analysis of rDNA sequence data yielded evidence for ancient divergence between the two taxa of *Blepharizonia* relative to timing of divergence between taxa in the sister-genus, *Hemizonia* (Fig. 3). Low interfertility of artificial hybrids corroborated phylogenetic evidence for greater divergence between the big tarweed taxa than implied by Keck's (1959) taxonomy.

Baldwin et al. (2001) concluded that the two taxa of *Blepharizonia* should continue to be recognized and warrant treatment as separate species, *B. laxa* (=*B. plumosa* subsp. *viscida*) and *B. plumosa* (=*B. plumosa* subsp. *plumosa*). Baldwin et al. (2001) also concluded from DNA and artificial hybridization data that natural hybridization between *B. laxa* and *B. plumosa* probably does not pose a threat to the continued existence of the rare big tarweed, *B. plumosa.* Preliminary evidence for phylogeographic diversity uncovered within the rare *B. plumosa* (Baldwin et al. 2001) should serve as a caution against any conceivable restoration efforts that involve moving germplasm of *B. plumosa* between populations (especially north or south of the Livermore Valley), at least until continuing studies of lineage diversity in *Blepharizonia* are completed.

Sidalcea keckii: A minor variant of *S. diploscypha* or a distinct, rare lineage?—Phylogenetic studies of *Sidalcea* (Malvaceae) by Andreasen (in prep.; see also Andreasen and Baldwin, 2001) helped to clarify evolutionary lineages in the genus, a group previously regarded as highly variable, taxonomically difficult, and in need of systematic attention (Hill 1993). Among the issues of conservation concern examined by Andreasen was the evolutionary status of *S. keckii,* a narrowly endemic species from Tulare County, California, long thought to be extinct until rediscovered in 1992 (see Skinner and Pavlik 1994). Assigning conservation priority to *S. keckii* has been complicated by uncertainty about
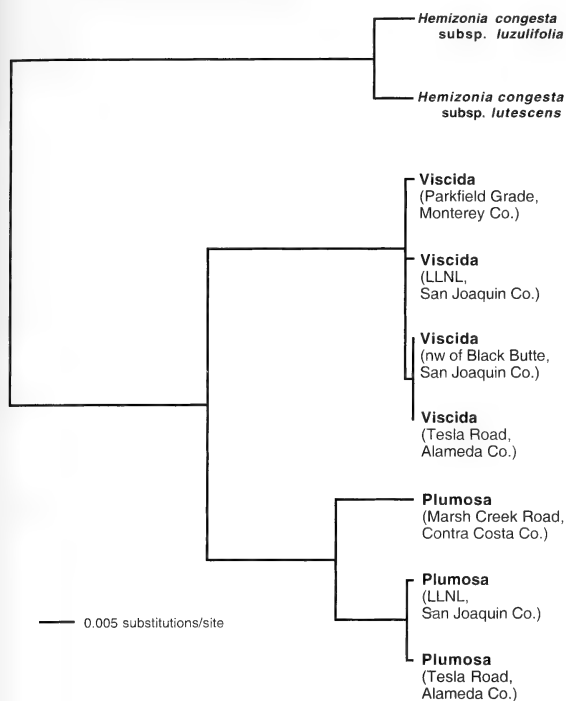
FIG. 3. Chronogram of one of two maximally parsimonious trees from phylogenetic analysis of nuclear ribosomal DNA sequences of *Blepharizonia* and *Hemizonia* (modified from Baldwin et al. 2001). Branch lengths were optimized by maximum-likelihood to conform to an hypothesis of evolutionary rate constancy, which could not be rejected using a tree-wide likelihood-ratio test. Note the extensive divergence between the two, minimally interfertile, mosaically sympatric taxa of *Blepharizonia* relative to divergence between the two representatives of *Hemizonia*. Biosystematic and phylogenetic data led Baldwin et al. (2001) to conclude that the two taxa of *Blepharizonia* each correspond to natural groups that warrant treatment as distinct species. Abbreviations: Plumosa = *B. plumosa sensu stricto* [=*B. plumosa* subsp. *plumosa*]; Viscida = *B. laxa* [=*B. plumosa* subsp. *viscida*]. See Baldwin et al. (2001) for tree statistics and support values.

distinctiveness of the species from the morphologically similar, widespread species *S. diploscypha*.

Andreasen (in prep.; see also Andreasen and Baldwin, 2001) sampled both species in a genus-wide phylogenetic analysis of rDNA spacer sequences in *Sidalcea*. She found that *S. diploscypha* and *S. keckii* were most closely related to one another, as expected, but that representatives of each species constituted highly divergent lineages. Based on her findings, Andreasen concluded that *S. keckii* is worthy of continued taxonomic recognition and conservation attention.

RECOMMENDATIONS FOR SYSTEMATIC STUDIES

To promote further progress by systematists in the discovery of plant diversity corresponding to minimal-rank taxa and in the refinement of plant

classification at the lowest taxonomic levels, the following recommendations are presented for planning systematic studies:

- *Sample widely within accepted taxa.* To test taxonomic hypotheses and to detect cryptic lineage diversity, sampling within taxa across the range of phenotypic variation and across the geographical and ecological distribution has been productive (see above). Examining only one exemplar per taxon cannot reveal hidden diversity or problems in circumscription at the taxonomic level of sampling.
- *Study herbarium collections.* Apart from yielding valuable data on morphological, ecological, and geographic variation within minimal-rank taxa, studies of herbarium specimens may reveal undescribed diversity more readily than new field exploration. Feasibility of extracting sufficient DNA for genetic analyses from small fragments of dried plant material may allow both morphological and molecular characterization of new species discovered in herbaria (e.g., Vargas et al. 1998).
- *Take seriously the old taxonomic literature.* A sampling focus on taxa recognized only in the most recent taxonomic revision of a plant group may ensure a repeat of errors made in that systematic treatment, especially if sampling within taxa is minimal. In addition to taking a fresh look at variation within a group, systematists may find that taxa no longer recognized in modern treatments represent evolutionary lineages warranting recognition (e.g., Chan 2000).
- *Voucher all specimens examined.* Vouchering specimens for systematic studies of groups corresponding to minimal-rank taxa is perhaps even more essential than for studies at higher taxonomic levels to ensure that the identities of sampled plants are not misinterpreted by others. Documentation of detailed collection data is also critical for studies involving fine-scale sampling within minimal-rank taxa (see Huber 1998).
- *Examine multiple lines of systematic evidence.* A single line of systematic evidence (e.g., one gene) can be potentially misleading about relationships within a group (see Wendel and Doyle 1998). Lineage sorting and hybridization are more likely to affect evolutionary patterns in young plant groups than in old lineages. Examining multiple, unlinked gene regions or molecular and other lines of data (e.g., morphology or cytology) should increase the likelihood of achieving an accurate understanding of natural plant groups.
- *Sample the rare taxa.* The potential value to conservation biology of gaining additional systematic data on rare plants makes the efforts required to sample rare taxa worthwhile. Most modern molecular systematic methods involve use of the polymerase chain reaction (PCR), which requires

only minimal DNA (see Hillis et al. 1996). Molecular data from rare plants can be obtained from minute amounts of fresh or dried (e.g., herbarium) tissue without impacting populations or significantly damaging voucher specimens.

- *Study biological characteristics of the plants.* Including an experimental biosystematic component (e.g., from artificial hybridizations or common gardens) and field component (e.g., pollination ecology, demography) in modern systematic studies can yield valuable biological data for resolving fine-scale diversity within a group and may lead to insights into evolutionary processes affecting diversification (see Baldwin 1995). Studies of population-genetic structure within lineages can provide critical biological data for resolving microevolutionary dynamics of populations and for refining conservation strategies (e.g., Bushakra et al. 1999).

- *Communicate with other field botanists.* Close communication and cooperation with professional and amateur field botanists is especially valuable for promoting discovery and conservation of plant diversity. The reciprocal flow of knowledge that can develop between systematists and other field-immersed plant biologists enriches botany in general and can lead to a more intensive, well-focused effort toward detecting and conserving diversity than would be otherwise possible (see Ertter 2000a, b).

- *Publish findings and follow through on taxonomic changes.* Other biologists, especially those involved in biodiversity assessment and conservation (e.g., Skinner and Pavlik 1994), rely on formal taxonomic treatments and other publications by the systematic community. Translating pertinent results of systematic studies into taxonomic changes is a potentially tedious but necessary step to ensure that newly discovered evolutionary lineages and new understanding of the circumscriptions and positions of monophyletic plant groups in general are recognized by others.

RECOMMENDATIONS TO THE CONSERVATION COMMUNITY

Based on the evidence from phylogenetic studies that circumscriptions of some minimal-rank taxa misrepresent or under-represent biodiversity, I suggest that the following recommendations be adopted by the conservation community in the interests of preventing loss of natural plant groups:

- *Regard taxa as hypotheses of natural groups subject to change.* Some refinements to our understanding of the composition and position of natural plant groups are inevitable and desirable to ensure that conservation efforts are well directed.

- *Accept and encourage taxonomic changes based on solid evidence of natural groups.* Although taxonomic changes create difficulties in database management and communication, changes that reflect an improved understanding of natural groups are valuable and worth adopting. From a conservation perspective, names are expendable; natural plant groups are irreplaceable.

- *Bear in mind that recognized species or infra-specific taxa are not necessarily minimal units of biodiversity.* As noted above, unrecognized, evolutionarily distinct lineages may exist within a species, subspecies, or variety (also see Soltis and Gitzendanner 1998). Research efforts to discern any undetected diversity within minimal-rank plant taxa using modern systematic approaches (e.g., phylogeographic studies) have been minimal (see above). Available data suggest that cryptic lineages often show some degree of geographic distinction (see Avise 2000). Efforts to protect taxa throughout their geographical and ecological ranges are therefore warranted not only to ensure survival of locally adapted populations and overall allelic diversity within a group (Endler 1977; Chesser 1983) but also to preserve potentially distinct evolutionary lineages.

- *Resist proposals to use non-local germplasm indiscriminately in restoration efforts.* Use of non-local germplasm in restoration efforts may result in extensive hybridization between evolutionarily distinct but cryptic lineages and consequent loss of biodiversity (see Storfer 1999). This concern is especially important given the increasing prevalence of mitigation efforts seeking to augment rare plant populations in protected areas with propagules or mature plants translocated from other populations slated for destruction. The well-intentioned practice of augmentation may be justifiable to prevent or overcome inbreeding depression, e.g., if the populations involved are remnants of a more continuous metapopulation fragmented by human-related activities or if geneological and population genetic data indicate that declining populations are of a common regional lineage and share similar genetic structure (see Moritz 1999). Indiscriminate translocation of plants from one population to another has potential to do much harm to biodiversity and to our prospects for understanding the evolution or population-genetic structure of natural plant populations.

In the absence of genealogical and population-genetic data, proposals for augmentation of natural populations with non-local seed should be viewed with the same skepticism as the universally objectionable idea of intermixing germplasm from unquestionably distinct but interfertile, naturally allopatric species. Even if the populations to be intermixed do not represent highly divergent evolutionary lineages, potential still exists for outbreeding depression from loss of local adaptation or breakdown of co-adapted gene complexes (see Templeton 1986; Slatkin 1987;

Moritz 1999; Storfer 1999). Planting of wild-flowers along roads and highways is another widespread practice with similar potential for re-ducing biodiversity and confounding scientific investigation of natural plant populations.

● *Consider cryptic biodiversity in conservation planning.* Even if systematists decline to recog-nize cryptic lineages as taxa, conservationists can plan for preservation of cryptic groups in the interests of preserving unnamed, as well as named, biodiversity. Under the U.S. Endangered Species Act, evolutionarily significant but mor-phologically indistinct and unnamed lineages of vertebrates are eligible for protection; similar protection for cryptic plant groups may be pos-sible to achieve. Geographical and ecological cri-teria have been used effectively for recognizing cryptic vertebrate lineages (e.g., salmonids) and also may be useful for identifying various cryptic plant groups.

CONCLUSIONS

The potential for modern systematics to play an important role in the discovery and conservation of fine-scale plant biodiversity is enormous and most-ly untapped. The movement of systematics toward use of molecular and phylogenetic methods has been perceived by some botanists as an alarming diversion from the urgent business of finding and describing previously undetected and, usually, en-dangered plant diversity ("fiddling while Rome burns"). I suggest that the use of modern system-atic approaches, far from posing a threat to ad-vancing our knowledge of fine-scale biodiversity, can be an invaluable means of achieving rapid progress in the discovery and conservation of plant lineages.

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THE NEED FOR INTEGRATED STUDIES OF THE CALIFORNIA FLORA

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ABSTRACT

The general field of systematic biology is an inclusive discipline that has taken great steps forward in the last two decades. New theories and methods have been developed for using character data to reconstruct phylogenetic relationships and thus improve classifications. Copious new sources of character data have become available from the molecular level. New analytical methods have been developed for using phylogenies to quantify biogeographic, ecological, and evolutionary patterns and test hypotheses about process. These new developments need to be integrated with traditional strengths in systematics such as collections-based research, floristics, and morphological/developmental studies, through greater communication and collaboration. Because of its unique geology and biology, its long and intense history of study, and its outstanding botanical institutions, California can serve as an ideal model for a newly integrated approach to systematic biology.

There is a danger, in this time of specialization and information overload, to become too narrowly entrenched in one's main activities. This happens in the botanical community of California: an in-the-trenches conservationist can get frustrated with an herbarium researcher because of taxonomic name changes that may on the surface seem aggravating and pointless. A consultant doing field inventories might not see the need for all the theory and heavy-duty computation applied in academic ecology these days. A systematist comfortable with morphological characters in a large part of the flora might be suspicious of the proliferation of molecular characters and cladograms. A molecular systematist might lose touch with the important morphological characters that should be useful for their work. Some professors in academia may get too far removed from the realities and training needs in the outside botanical community. The list could go on, but I hope the main take-home message is clear: we need some mutual enlightenment and understanding.

The study of plant systematics and evolution is an integrated whole. We need the floristic specialists with their good field knowledge of geography and variation in plants. We need to add molecular characters to the mix, while not losing the ability to gather, evaluate, and use morphological and anatomical characters. We need a strong, well-justified theoretical framework within which to test hypotheses. We need the powerful new analytic tools available in ecology and systematics to look at community structure and phylogenetic trees in more sophisticated ways. And most of all, we need to develop the best understanding we can of the flora at all levels, communicate it clearly to the relevant communities, and apply it to the urgent conservation needs facing California (see also Baldwin 2000). Thanks to Jepson's foresight in creating a practical botanical institution in the center of an

academic hotbed, the Jepson Herbarium is perfectly placed to span these different approaches and encourage much needed integrated studies, which we attempted to do with this symposium.

The field of systematic biology has taken great steps forward in the last two decades, in three major areas. One major step forward has come about through the introduction of new theories and methods for using character data to reconstruct phylogenetic relationships and thus improve classifications. The second major step forward was the introduction of copious new sources of character data from the molecular level. The third major step forward was in the development of analytical methods to use phylogenies to quantify biogeographic, ecological, and evolutionary patterns and test hypotheses about process. I will go into each of these new developments in turn, with the goal being to show how they can be integrated with traditional strengths in systematics such as collections-based research, floristics, and morphological/developmental studies to yield a truly integrated approach.

Phylogenetic Systematics

The need for phylogenetic classification. The main developments in systematic theory stem from the phylogenetic approach developed by Hennig (1966). I summarized the new developments in *Madroño* in 1995, and they have been well outlined elsewhere in texts and reviews (Farris 1983; Sober 1988; Forey et al. 1992; Maddison and Maddison 1992; Mishler 1994, 2000). A quick outline should thus suffice here: the fundamental idea is that phylogenetic branching events among lineages should be reconstructed using shared, homologous *markers* (Mishler 2000). The markers are characters that changed state along a lineage, thus serving as evidence in the future that the lineage once existed. The derived state of a marker when shared among

contemporaneous taxa (called a synapomorphy) can thus be used to postulate the existence of a once-shared lineage uniting them. This hypothesis can be tested by other putative synapomorphies, and so on. In Hennigian systematics, classification follows the reconstruction of a well-supported phylogeny, and only hypothesized monophyletic groups should be named—these are groups that consist of all and only descendents of a common ancestor. Thus in current thinking there is a fundamental isomorphism among synapomorphy, monophyly, and named taxa.

Why has this three-fold parallelism been so widely accepted across the community? Phylogenetic classifications may not always be the most practical, that is the synapomorphic characteristics may sometimes be hard to detect easily. There is an element of human choice in what we use our formal Linnaean nomenclatorial system for, so why choose phylogeny as a basis? To answer this question requires an examination of what classifications are for. Evolution is real, as are organisms (physiological units), lineages (phylogenetic units), and demes (interbreeding units), for example. On the other hand, our classification systems are obviously human constructs, meant to serve certain purposes of our own: communication, data storage and retrieval, predictivity, and studies of process. While the last purpose seems perhaps the most esoteric, the most important function of a classification is its theoretical meaning, as discussed by Mishler (2000). A classification should capture units participating in the most important causal processes operating in the system. In this way the classification will be maximally predictive and useful for practical and theoretical purposes. In biology, our best understanding is that evolution is the most important process organizing biological diversity, and thus the field of systematics in general has settled on restricting the use of formal taxonomic names to represent phylogenetically natural, monophyletic groups. While this is a widely understood standard for modern systematics, recent developments in two areas deserve further, more detailed, discussion: species concepts and rank-free classification.

Species. Given the above arguments, what should the species rank represent in the Linnaean classification system? There are two necessary parts to any species definition. The criteria by which organisms are *grouped* into taxa must be specified, as well as the criteria by which a taxon is *ranked* as a species rather than some other hierarchical level. Following the arguments given above supporting a Hennigian phylogenetic system of classification in general, the *grouping* criterion that should be used at the species level, as at all other levels, is monophyly (Mishler and Theriot 2000). Under this view, apomorphies are considered to be the necessary empirical evidence for unambiguous phylogenetic species, as for phylogenetic taxa of all ranks. It follows that re-productive criteria cannot be used to group organisms into phylogenetic species. The fundamental inappropriateness of using breeding compatibility in cladistic analysis is because the ability to interbreed (potential or actual) is a symplesiomorphy (i.e., shared primitive characteristic) by definition, thus not a phylogenetically valid grouping criterion. The species *ranking* decision is currently forced because systematists have legislatively constrained themselves to use a ranked Linnaean hierarchy (see the following section for a possible alternative). The ranking criteria for species should involve practical criteria such as the amount of character support for a group; the species could then be viewed as the smallest hypothesized monophyletic group with good support (the minimum-rank taxon—see Baldwin 2000, this issue). The species ranking decision may also involve biological criteria in better known organisms, including reproductive criteria, e.g., the origin of a distinctive mating system at a particular node or the acquisition of *exclusivity* (a condition in which each allele in a lineage is more closely related to another allele in the lineage than it is to an allele outside the lineage; Baum and Shaw 1995; Graybeal 1995).

There are, of course, difficulties applying the concept of monophyly at this level. There are a number of different sources of homoplasy (incongruence between certain character distributions and the cladogram based on maximum parsimony), such as adaptive convergence, gene conversion, developmental constraints, mistaken coding, lineage sorting, reticulation, etc. The last named factor is the most problematical because it involves the fundamental model of reality underlying cladistic analysis—the other factors are cases of mistaken hypotheses of homology, whereas "homoplastic" character distributions due to reticulate evolution involve true homologies whose mode of transmission is not tree-like.

As less inclusive levels in the genealogical hierarchy are considered there is an increasing probability that reticulating ("hybridizing") events will occur, rather than the diverging phylogenetic relationships assumed by the cladistic approach. However, the problem of reticulation is not confined to the species level; indeed, reticulation can occur throughout the hierarchy of life, and so is a problem of more general difficulty, and one that is receiving more attention by systematists (e.g., McDade 1990, 1992). It is becoming clear that while a certain amount of reticulation does not preclude cladistic reconstructions of phylogeny, extensive reticulation can cause major problems. We can reconstruct relationships in the face of *some* amount of reticulation (how much is not yet established, but is amenable to study, e.g., McDade 1992). As with convergence, where the application of cladistic analysis provides the only rigorous basis we have for identifying homoplasy and thus demonstrating non-parsimonious evolution, the only way we can identify

reticulation on the basis of character analysis alone is through the application of cladistic parsimony, followed by examination of homoplasy to attempt to discover its source (see discussion by Vrana and Wheeler 1992; Mishler and Theriot 2000). How modes of reticulation actually affect character distributions on cladograms is a productive avenue for empirical and theoretical investigations.

To summarize, a *phylogenetic species concept* (Mishler and Theriot 2000; not to be confused with the different phylogenetic species concepts of Cracraft 1983; Nixon and Wheeler 1990) can be defined based on the following considerations. First, organisms should be grouped into taxa at all levels (including the lowest level, species) on the basis of evidence for monophyly; breeding criteria in particular are not useful for grouping purposes. Second, criteria used to assign species rank to certain monophyletic groups must vary among different organisms, but might well include ecological criteria or presence of breeding barriers in particular cases (see Mishler and Brandon 1987; Mishler and Theriot 2000 for elaboration).

The need for rank-free classification. The above discussion assumes that the current Linnaean system of ranked classifications is to remain in place, thus the species ranking decision is forced because systematists have constrained themselves to use a ranked Linnaean hierarchy. An intriguing possibility has arisen through recent suggestions for reforming the Linnaean system by removing the concept of ranks (De Queiroz and Gauthier 1992). This proposed change would keep the hierarchy of named phylogenetic groups, but remove the ranks (including species) associated with the names. This would remove the arbitrariness of ranking decisions at the "species level" (Mishler 1999).

As the community has applied phylogenetic analysis broadly at many levels, it has become clear that the ranks in the Linnaean system (orders, families, genera, etc.) are problematic for classification. The many changes that are needed to bring classification into line with our understanding of phylogeny, plus the sheer number of levels being resolved in the tree of life, have made the current system of nomenclature appear a bit outdated. There are not nearly enough ranks to suffice in classifying the tree of life, with its millions of branches.

Furthermore, there are practical problems with the use of ranks. Most aspects of the current code, including priority, revolve around the ranks, which leads to instability of usage. The need to maintain the hierarchy of the ranks leads to names being changed without good reason. For example, when a change in relationships is discovered, say a current family is found to be nested cladistically inside another family, several names often need to be changed to adjust, including the names of groups whose circumscription has not changed. Frivolous changes in names often occur under the current code, when authors merely change the rank of a group without any change in postulated relationships at all.

The most important problem with ranked classifications are that they lead to bad science, if a user of a classification naively assumes that taxa at the same rank are comparable in some way. The existing, ranked Linnaean nomenclatorial system is based on a non-evolutionary world-view (with taxa at the same rank being somehow equivalent in the mind of the creator). Under an evolutionary worldview, the ranks don't make sense. Practicing systematists know that groups given the same rank across biology are not comparable in any way (i.e., in age, size, amount of divergence, diversity within, etc.), but many users of classifications do not know this. For example, ecologists or paleobiologists often count numbers of taxa at a particular rank as an erroneous measure of "biodiversity."

I have argued (Mishler 1999) that the formal ranks should be abandoned (including the species rank), for efficient and accurate representation of phylogenetic relationships. Instead, names of clades should be hierarchically nested uninomials regarded as proper names (although current usage should be followed as much as possible to retain links to the literature and collections). A clade should retain its name regardless of whether new knowledge might change its phylogenetic position, thus increasing nomenclatorial stability. Furthermore, since clade names would be presented to the community without attached ranks, users would be encouraged to look at the actual attributes of the clades they compare, thus improving research in comparative biology. In the future, I hope that "rank-free" phylogenetic taxonomy will allow efficient presentation of theoretically justified, maximally useful classifications that will unify biology by providing a single, consistent framework for the study of evolutionary and ecological processes at all levels.

Molecular Data

Many new data sets have been added to systematics because of the availability of technology from molecular biology that allows relatively easy comparative sequencing of genes (Soltis et al. 1998). It is important to note at the outset that these new molecular data are not meant to *replace* traditional morphological and anatomical characters in systematics. On the contrary, a number of recent studies in the field have shown that molecular characters, while a very useful addition to systematics, are *complementary* to the traditionally used characters. These new characters should be added to appropriate morphological characters and used to improve our knowledge of plant relationships, including species circumscriptions as well as relationships among species, genera, and families. In turn, improved understanding of relationships is necessary

to inform our practical uses of plants and our conservation efforts.

Various laboratory techniques have been developed for molecular systematic studies. Some of these, such as DNA hybridization and restriction fragment length polymorphisms (RFLPs) yield only distance information, which is difficult to apply to phylogenetic tree reconstruction since information about individual homologies is missing. Other techniques, including mapping of restriction enzyme sites and direct DNA sequencing methods, yield information about specific characters. The latter techniques are thus more heavily favored, because character-based methods (based on explicit evolutionary models of homology) provide markers suitable for phylogenetic analysis, as described above.

Speaking generally, molecular data do have a number of advantages for systematic studies (Mishler 1994). A large number of molecular characters is available for any given level of phylogenetic inference, which has proven to lead in many cases to increasingly better-supported hypotheses of relationships. This advantage seems particularly true at low taxonomic levels, even within species, where morphological characters tend to be subtle and hard to define. On the other hand, molecular data have some disadvantages as well. There are problems with sampling at the molecular level—it is time consuming and expensive to sample within study taxa (to check for polymorphism) at the level that is possible for many morphological characters, and, of course, fossil taxa generally cannot be included. Point mutations in DNA are simple characters with few possible character-states, subject to parallel changes that can't be detected easily except through their congruence with other characters on a cladogram.

Morphological characters have a number of advantages of their own (Mishler 1994). They are often complex in structure and development, with many possible character-states, thus allowing better supported initial hypotheses of homology. Sampling within study taxa to understand polymorphism is often easier and cheaper than with molecular data. Many key morphological characters can be seen in well-preserved fossils, thus allowing inclusion of completely extinct lineages, which can be essential to getting the correct tree. Morphological characters are, of course, subject to their own difficulties of interpretation, as compared to molecular data. There are usually many fewer characters, variation patterns can often be difficult to organize into discrete character-states, and convergence can lead to mistaken hypotheses of homology (of course, congruence can plague molecular characters as well).

The generalized strengths and weaknesses of molecular and morphological data are complementary to a large extent. Thus, the best approach, of course, is to apply appropriate characters from all levels of organization to some specific problem of relationships. Molecular characters will remain essential as the bulk of available evidence, particularly for shallower branching events. Morphological characters will also remain critical pieces of evidence for many branch points in evolutionary history, particularly the deeper ones; plus they are essential for integrating fossils into evolutionary trees and of course for identification purposes in practical applications of systematics such as floristics. Thus, the future clearly lies in studies integrating both sources of data.

Comparative Biology

The interplay and contrast between phylogenetic and functional/structural groupings has ushered in a new era of scientific rigor in comparative biology with the development of explicit and testable hypotheses of phylogenetic relationships. Many advances have been made in improving evolutionary model building as a route to understanding; "tree-thinking" is now central to all areas of systematics and evolution. The central importance of phylogeny reconstruction in systematics, ecology, and evolutionary biology has become widely realized in recent years (Donoghue 1989; Funk and Brooks 1990; Wanntorp et al. 1990; Brooks and McLennan 1991; Harvey and Pagel 1991; Miles and Dunham 1993; Martins 1996). Explicit cladistic phylogenies now provide a critical basis for classification as well as for studies of speciation, biogeography, ecology, and behavior (among many other areas).

The area of phylogenetic comparative methods is one of considerable controversy and rapid conceptual development. Virtually every issue of major journals and each new book on systematics and evolution contains something of interest on this subject. The general working procedure is to first carefully define the causal hypothesis to be tested, then specify a null hypothesis (what you would expect if the hypothesized cause is not working), and finally design a phylogenetic test that would let you reject the null hypothesis if it is indeed false.

The large number of comparative methods can best be summarized by placing them into categories corresponding to the types of hypotheses meant to be tested, as addressed below.

Comparing cladograms. These methods are meant for comparing different phylogenetic trees in the study of *coevolution.* Coevolution can be broadly defined as congruence between two or more systems undergoing tree-like evolution (i.e., evolution by descent with modification). This is a generalization of the phylogeny/homology relationship (i.e., the "coevolution" of organism lineages and characters discussed above). Coevolution comes in many forms: vicariance biogeography (organism/earth coevolution), host/parasite relationships, community evolution (e.g., symbionts, pollinator/plant coevolution, or other long-term ecological associations).

Biogeography can serve as an example of the concept of comparing trees for their mutual information content. Historical biogeography has a long tradition in biology, and was indeed a major source of evidence for Darwin. After evolution became widely established as a principle, the initial approach to biogeography was to look for areas of origin and dispersal patterns based on stable world geography (see Wiley 1981). The work of Hennig (1966) led to the development of *phylogenetic biogeography*, which examined the distribution of *one* group at a time in relation to a cladogram. One famous outcome was Hennig's "progression rule," the observation that more derived species often tend to occur further from the initial area of a lineage following speciation by peripheral isolation. The phylogenetic examination of *many* groups at a time can be traced to the works of Croizot following a method he called "panbiogeography"—a search for generalized distributional "tracks." This search for matching geographic patterns led to the approach called *vicariance biogeography,* a search for sister groups sharing the same pattern across many cladograms (Nelson and Platnick 1981).

The basic idea is to look for common patterns (and causes) of distribution—evidence from other organismal distributions can be relevant to understanding the distribution of a particular group! Congruence is taken as evidence of shared biogeographic history (vicariance); incongruence as evidence of separate history (dispersal). Methodologies have diversified to compare cladograms in coevolutionary studies, including consensus techniques (Funk and Brooks 1990), tree-to-tree distance metrics (Penny and Hendy 1985), and parsimony techniques (such as Brooks parsimony; see Brooks 1990; Brooks and McLennan 1991).

Comparing clades within a cladogram. These methods are meant to detect whether there are imbalances in symmetry between sister clades in the same cladogram, in order to address various questions in both micro- and macro-evolution. First of all, however, what is the null expectation? Intuitively, one might expect balanced trees, perhaps, based on some sort of false analogy to coin flips. But is this a correct assumption? "Random" trees can be generated in many ways (Maddison and Maddison 1992), and include equiprobable trees (picked out of a set of all possible trees—bias towards asymmetry), random joining trees (models a random speciation process—intermediate bias), or a random partition (bias towards symmetry). Using a Yule "pure birth" Markovian model to grow random trees, Slowinski and Guyer (1989) showed a nonintuitive result: the probability of each way of partitioning taxa at a bifurcating node is equal [for n terminal taxa, the probability of generating any division of species above a node into sister lineages of unequal size is $2/(n - 1)$; the probability is $1/(n - 1)$ for evenly divided sister lineages]. Thus, even

a node in which one species is the sister taxon to 39 other species is not significantly unbalanced at the $P = 0.05$ level ($P > 0.051$).

This work has lead to the realization that real trees should be expected to be quite asymmetrical even under a random model. Furthermore, even if trees are judged significantly asymmetric, how can we associate that judgement with some specific factor postulated to be the cause of that asymmetry? That leads to the hot topics of "key innovations" and "adaptive radiations." There have been many, often conflicting definitions of *adaptive radiations* (Givnish and Sytsma 1997). Decomposing the term is best, and suggests that "adaptation" needs to be established separately from "radiation." The rapid diversification of lineages (caused by a postulated "key innovation") should be accompanied by ecological, morphological, and/or genetic diversification. A number of methods have been developed to deal with the required time estimation problem, which involves two questions: Can we assume a molecular clock? If we can, how do we calibrate it (Sanderson and Wojciechowski 1996; Sanderson 1997; Baldwin and Sanderson 1998)?

Discrete-state character comparisons on a cladogram. These methods are meant for examining how discrete-state characters evolve on a tree individually and together. Such characters can be mapped onto cladograms using parsimony, so as to minimize the number of character-state changes. In this way, suites of characters are built up for Hypothetical Taxonomic Units (HTU's). Specific types of hypotheses that can be tested include polarity of character-state changes in one character, and the association of state changes in two characters, either undirected (Ridley's test; Ridley 1983) or directed (Maddison's test; Maddison and Maddison 1992).

Most of these studies are motivated by the search for *adaptation.* There is a long-standing observation that organisms tend to match their environment. Darwin and many Darwinians thought that all structures must be adaptive for something. But this assumption has come under severe challenge in recent years (Gould and Lewontin 1979). Not all structures and functions are adaptive. In fact, there are very few completely demonstrated examples of adaptations.

The definition of adaptation in a formal sense requires fulfillment of four different criteria (Mishler 1988; Brandon 1990):

1. Engineering. Structure must indeed function in hypothesized sense. Requires functional tests.
2. Heritability. Differences between organisms must be passed on to offspring, at least probabilistically. Requires heritability tests (parent-offspring correlations; common garden studies).
3. Natural Selection. Difference in fitness must occur because of differences in possession of the hypothesized adaptation in a common environment. Requires fitness tests.

4. Phylogeny. Hypothesized adaptive state must have evolved in the context of the hypothesized cause. Requires phylogenetic tests.

Only something that passes all these tests is an *adaptation*. If it passes tests 1–3, it can be called an *aptation*. If it then fails test 4 it can be called an *exaptation* (Gould and Vrba 1982). Thus, a phylogenetic test, while not sufficient in itself, is necessary as part of a complete adaptive explanation (Coddington 1988; Mishler 1988; Donoghue 1989).

Continuous character comparisons on a cladogram. These methods are meant for examining how quantitatively varying characters are associated on phylogenies. Note that these are characters that do not meet the 'discrete-state' criteria for taxonomic characters. The "bad old way" to compare two such characters was through direct correlations of species values (using species as data points). However, as pointed out by Felsenstein (1985) and others, this treats species as if they are all equally related to each other. The advent of quantitative comparative approaches was motivated by attempting to "remove" the influence of history, for example using ANOVA and ANCOVA (Harvey and Pagel 1991), autocorrelation (Cheverud and Dow 1985), independent contrasts (Felsenstein 1985; Burt 1989), and general linear model approaches to partition variance and "subtract" the phylogenetic effects (Martins 1996). Conversely, other methods explicitly describe variation due to phylogeny by tracing the quantitative characters on a phylogenetic tree, reconstructing values for nodes, and looking at direction of change by comparing ancestors and descendants (e.g., Huey and Bennett 1987).

The Integrative Approach

These diverse sources of data, complex theories, mathematically complicated algorithms, and multiple approaches to analysis have reinvigorated the field of plant systematics, yet at the same time they have made the field more complex and harder to master. No one person can keep ahead of all these parts of the whole endeavor. Thus, there will be an increasing need for mutual understanding among specialists, increased collaborative research, and more sharing of expertise. Training of students must continue to diversify into all the new approaches, while at the same time not losing sight of older, still valuable approaches. Botanical institutions need to adapt and expand their vision and capabilities. Our ultimate goal for the next 50 years of California botany should be to serve as a model by developing integrated studies that combine all these approaches and presenting this information in easily accessible ways to the public.

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OUR UNDISCOVERED HERITAGE: PAST AND FUTURE PROSPECTS FOR SPECIES-LEVEL BOTANICAL INVENTORY

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Abstract

On-going botanical field exploration and the synthesis of resultant data into species-level plant distribution information in the United States has been handicapped by multiple assumptions: results of such an effort would have little or no pragmatic implication; all necessary work has already been completed, and the resultant information just needs to be compiled within a modern informatics framework; herbarium vouchers are not only already sufficient but become peripheral once label data are captured; further contribution by the systematics community is likewise peripheral, except for a trickle of new species descriptions that can be readily accommodated; species-level field exploration within the United States is neither science nor fundable; and a comprehensive species-level inventory is simply too big a project to tackle. To address these assumptions, a brief account of botanical surveys contemporaneous with topographic mapping efforts of the U.S. Geological Survey is presented, with parallels drawn where possible. Botanical inventory efforts of the University of California at Berkeley are likewise presented, including involvement in Wieslander's Vegetation Type Mapping Project and Bailey and Bailey's project to map the vegetation of Western National Parks. The cumulative result of these and other efforts, however, leave us with an estimated 5% of the national vascular flora still to be described, and distributional information of the known species falling far short of what is needed for informed decision-making. Simple accretion of additional distributional reports is not sufficient, but needs to be based on vouchered reports that have been critically evaluated within taxonomic models by members of the systematics community. The conclusion is therefore that standing assumptions are unjustified, and that a large-scale biodiversity counterpart to the topographic efforts of the U.S. Geological Survey is in fact a realistic and desirable goal.

During this past century, organized field exploration of botanical diversity and the synthesis of resultant data into species-level plant distribution information in the United States have become somewhat passé, at least in scientific realms. At best, earlier cataloguing of species has been transcended by vegetation mapping efforts undertaken by plant ecologists, often completely decoupled from plant systematists who are expected to focus on phylogenetic analyses. As addressed by subsequent papers in this symposium (i.e., Baldwin [2000], Charlet [2000]), both phylogenetic analysis and vegetation mapping represent extremely productive arenas of research, having conservation and land management significance well beyond pure science. The question nevertheless needs to be answered: should the age of species-level botanical surveys indeed be properly relegated to the past, or is there instead not only a legitimate opportunity but a crying need for seriously supported species-level field exploration and the synthesis of resultant information within a scientifically valid framework?

To answer this question, one must first analyze the real and perceived obstacles to species-level botanical inventory in the United States. Prominent among these would be the following assumptions:

- The results of such an effort would have little or no pragmatic implication.

- All necessary work has already been completed, and the resultant information just needs to be compiled within a modern informatics framework.

- Herbarium vouchers are not only already sufficient, but become peripheral once label data are captured.

- Further contribution by the systematics community is likewise peripheral, except for a trickle of new species descriptions which can be readily accommodated by the environmental sciences and informatics communities.

- Species-level plant inventory in the United States is not sufficiently scientific, innovative, or otherwise high-profile to merit funding.

- A comprehensive species-level inventory is simply too big a project to tackle (hence the shortcuts of vegetation mapping, indicator species, umbrella species, etc.)

Just how valid are these assumptions? Are they supported by either the historical record or modern-day realities? And if not valid, what are the implications for such modern-day issues as biodiversity conservation, which relies heavily on comprehensive, accurate distributional information as the basis for critical land-management decisions? The purpose of the current paper is to address these questions, beginning with (and leaning heavily on) the historical context and precedents.

LESSONS FROM THE PAST

The fate of national surveys. When a modern biologist is presented with the question, 'What newly-established systematic survey of the United States was dealt a serious set-back by a hostile Congress on the grounds of being unrealistically ambitious, too costly and long-lasting, scientifically suspect, of limited (or negative) value, too much power concentrated in a single federal bureaucracy, contrary to the ideals of private property and free-market enterprise, and a threat to western state's rights?' the abortive attempt to establish a National Biological Survey in the early 1990's readily comes to mind. This ambitious proposal, outlined by the National Research Council of the National Academy of Sciences (1993), was a primary target of the heavily conservative 104th Congress's 'Contract with America,' surviving on a significantly diminished scale within the United States Geological Survey (USGS) (Wagner 1999). Although the resultant Biological Resources Division, established in 1996, has certainly generated its share of solid biological research, the discrepancy between the original vision and the eventual outcome left the concept of a full-fledged biodiversity survey of the nation discredited, and many of its proponents disheartened.

What has been forgotten, however, is that the description applies equally well to the founding of that venerable institution, the USGS itself, under the directorship of John Wesley Powell. Although Powell is best known nowadays for his heroic exploration of the Grand Canyon, his biography by Stegner (1953) illuminates clearly the pivotal role that Powell played in the development of land management principles and governmental agencies that went hand-in-hand with the settlement of the western United States. Powell advocated comprehensive topographic mapping of areas being opened for settlement as an essential precursor to rationale land-use planning. He focused particularly on water rights and grazing allocations, recommending Mormon-style cooperative irrigation districts and 2500 acre grazing units (Goetzmann 1966). These proposals, however, were not well received by the majority of Westerners at the time, giving rise to protracted political battles that remain part of our present legacy.

Nevertheless, in spite of vehement opposition to Powell's vision and efforts, the long-term result in the topographic realm was success beyond Powell's most ambitious dream. As noted by Stegner (1953), seven decades after the initiation of the USGS over half of the United States had been topographically mapped, but only about one-fourth on the scale needed for contemporary planning. As a result, in 1953 there were more than two dozen government bureaus engaged wholly or partially in the preparation and printing and use of maps. Stegner also noted that this success resulted in spite of Powell's gross under-estimation of the task (i.e., 24 years at

a cost of $18 million), and that even though 'Some members of Congress a little later were ready to bet him that he couldn't do it in a hundred years for a hundred million . . . they ignored what was palpably true, that the maps were worth anything they cost, and more' (p. 280). If a parallel effort had been undertaken for biological mapping over the same span of time, would we now likewise take for granted the worthiness of the effort and value of the results?

The California geological survey. As it happens, various state and federally sponsored surveys that served as precursors to the USGS had generally included a biological component. As a prime example, the California Geological Survey (CGS) of 1860–1873, under the direction of J. D. Whitney, included in its mission 'a full and scientific description of its rocks, fossils, soils, and minerals, and of its botanical and zoological productions, together with specimens of the same, which specimens shall be properly labeled and arranged, and deposited in such place as shall be hereafter provided for that purpose by the legislature' (quoted in Brewster 1909, p. 185). In contrast to the USGS, state surveys in general enjoyed widespread support as 'a hallmark of enlightened state administration, a source of local cultural pride, and the means whereby exploitable resources might be cheaply located and advertised to would-be investors' (Goetzmann 1966, p. 355). The CGS likewise enjoyed public acclaim initially, but popular support quickly dwindled when the anticipated flood of economic benefits did not immediately materialize. As bemoaned by Whitney: 'State officers would be my best friends if I would be their confidential adviser in their interest in claims and stocks, but as it is, I do not know one of them who cares a rye-straw for the work [of the Survey]' (quoted in Leviton and Aldrich 1997, p. 66).

The prolonged decline of the CGS, as a result of political and economic interests independent of scientific value, left Whitney increasingly dispirited and disillusioned. This progression is wonderfully captured in a series of letters from Whitney to his brother, with a political cynicism that still resonates strongly (quoted in Brewster 1909, pp. 264–266):

26 February 1868: The prospects of the survey remain as uncertain as ever. Two committees have been at the office and exhibited even more than their usual amount of stupidity and ignorance. Since the Yosemite Valley bill passed over the Governor's veto, I feel so disgusted with California that I can hardly stand it much longer. Still I am running the survey along in a small way at my own expense, waiting to see what the jackasses at Sacramento will do.

29 March 1868: We have had a nice little time of it in the legislature. The petroleum and other swindlers made a dead set against the survey and

killed it, having malleable material to work with in the Democratic legislature. . . . We were especially unfortunate in having in the Senate . . . a former United States Surveyor General, under whose administration the fraudulent surveys in the southern part of the state were made, and the character of which is being exposed as fast as our work covers the ground. Of course he found against us with all his might.

And finally (pp. 289–290):

19 March 1874: The survey has succumbed to the stupidity and malignity of the legislature, backed by the same characteristics on the part of the Governor. . . . My own feelings are decidedly those of relief at getting the survey off my hands, with no fault of *laches* of my own, for it is *hard work* making a creditable thing of it on a small amount of money. I have always got more curses than coppers out of it.

Also working against the CGS, and as a parallel to Powell, Whitney himself had drastically underestimated the scale, to the extent that it was impossible for him to follow through on what he had originally promised:

I have found out that the State of California is a prodigiously large one. Not that I did not know it before; but now I have a realizing sense of it. It is as big as Great Britain, Ireland, Belgium, Hanover, and Bavaria put together! If I had a complete map of the state, a corps twice as large as I now have, and worked as fast (on the geology only) as the English government surveyors do, I should finish in just 150 years. Having our own maps to make, our labor is tripled; and consequently we shall be through in 450 years or thereabouts.
                (quoted in Brewster 1909, pp. 197–198)

With various ups-and-downs and overall dwindling support, the CGS nevertheless struggled along until finally giving up the ghost in 1873. The biological component, however, had been eliminated some years earlier. The initial survey crew included William H. Brewer as both botanist and Whitney's second-in-command. When Brewer departed in 1864 to accept a professorship in Yale, he was never replaced in kind. Instead, Henry N. Bolander was hired on a contract basis, as funding allowed, to do botanical surveys in parts of the state unvisited by Brewer (Jepson 1898; Ertter 2000b). The several thousand specimens accumulated by Brewer, Bolander, and others formed the basis for the first complete flora of California (Brewer et al. 1876; Watson 1880), compiled at Harvard University by Brewer, Asa Gray, and Sereno Watson, with treatments of specific groups (e.g., mosses) provided by an appropriate specialist.

Although the original state legislation mandated that the reports of the CGS be copyrighted and sold for the benefit of the common school fund, no funds were allocated, so that Brewer's efforts took the form of a labor of love:

I received no pay whatever after the closing of my connection with the Survey of California, neither for the time nor the expense in working up results. I spent an aggregate of two years time, a little more rather than less, and over two thousand dollars in cash, besides deducting another one thousand dollars from my salary from college because of time taken out from my work, that is, absence during term time at work on my plants at the Cambridge Herbarium.
                (quoted in Farquhar 1930, p. xxiii)

Whitney was eventually able to secure additional State funding for the publication of several Survey reports, but not for botany. Instead, a select group of California's wealthier citizens, including Leland Stanford, provided the necessary funds from their own pockets (Brewer et al. 1876).

The key lesson to be learned from this look at the history of the CGS, and the fate of the biological component in particular, is that termination of support resulted not from completion of the scientific goals, but because of unmet expectations, special interests, and pure politics. We can only wonder what legacy of critical biodiversity information would have accrued if the California Geological Survey had continued to the present, as has been the situation in several other states (e.g., Illinois, New York). Perhaps, as noted by Brewster (1909), the collapse of the CGS was inevitable at the time:

California, in 1860 when the survey began, looked to a future of unlimited growth and prosperity, and cut its coat according to the cloth it expected to own. Its actual lot was flood and drought, and the Civil War. Under these changed conditions, there were many well-intentioned persons who felt that elaborate, hand-colored monographs on birds and land-shells were not the things the young state needed most. As it turned out, the California Survey, on the scale on which Whitney planned it, was distinctly premature.   (p. 301)

Valid as Brewster's evaluation may have been to California of the late 19th century, it rings hollow in the face of early 21st century realities. Political and economic interests remain, but one can no longer argue that a full-fledged biological survey of California, as envisioned by Whitney and as called for by the state legislature in 1860, would still be 'premature.'

National biological surveys contemporaneous with the USGS. Federally supported surveys of

western lands began with the Lewis and Clark expedition of 1804–1806 and reached a heyday in the mid-1800's with a broad selection of surveys for railroad routes, boundary delimitations, and general exploration. Most of these surveys included a botanical component and are an important part of the historical record. The focus here, however, is on biological surveys that were contemporaneous with the USGS and that could potentially have served as counterparts.

As well described by Goetzmann (1966), the USGS resulted from the coalescence of three competing federally-sponsored surveys in the 1870's: that of Lieutenant George Montague Wheeler, representing the last attempt by the military to hold onto its former domination of western exploration; those led by Ferdinand Vandiveer Hayden under the aegis of the fledgling Interior Department; and the early efforts of Powell himself, backed by a diversity of sources, both private and government, and including the scientific community as represented by the Smithsonian Institution. Each of these three pre-USGS surveys contained a botanical component, with that of Powell's being weakest, and none providing more than the scantiest opportunity for collecting. This can be seen in the report by Townshend Stith Brandegee, whose botanical career began as part of the Hayden expeditions:

> Attached to the division of the San Juan as assistant topographer, as much time as possible was given to the botany of the country through which our work obliged us to pass. Under such circumstances, it was impossible to make a complete botanical collection of the district to our division; therefore no plants were gathered excepting such as seemed to be additions to the flora of Colorado, as published by the Survey in Miscellaneous Publications, No. 4 [Porter & Coulter, 1874]. The collections and notes were almost all made while riding from one topographical station to another.   (Brandegee 1876)

J. T. Rothrock, who joined Wheeler's expedition as botanist-surgeon in 1873 (Kelly 1914), not only collected plants for systematic analysis, but also helped initiate a new dimension of botanical survey by addressing economic aspects of the vegetation. Rothrock's reports included a forerunner of a conservation ethic (at least within the context of the time), quotes by Muir, and (similar to Powell) suggestions that governmental involvement might be appropriate: e.g., 'In view . . . of the acknowledged fact that in our older and more densely populated States we have an impending dearth of timber, would not a wise political economy endeavor to obviate such a result in our Western regions? Tree destruction began with us as a necessity, but it has been matured into an instinct' (Rothrock 1878, p. 34). According to Goetzmann (1966), similar attitudes characterized both Whitney and Wheeler, presaging the battles fought by Powell.

George Vasey, who accompanied Powell's 1868 expedition (Canby and Rose 1893), was in 1872 appointed Botanist to the U.S. Department of Agriculture (USDA), which at that time housed the botanical collections that had accumulated from various exploring expeditions. These collections had been in the custody of John Torrey at Columbia College in New York, with additional oversight provided by Asa Gray as a Regent of the Smithsonian Institution. A few years before his death, Torrey relinquished custodianship, and, in lieu of suitable facilities in the Smithsonian building itself, the collections were deposited with the USDA in 1868. They were not turned over to the Smithsonian Institution until 1894, to be merged with a separate plant collection that had been initiated by Lester Ward, paleobotanist for USGS, giving rise to the U.S. National Herbarium (Morton and Stern 1966).

Vasey replaced Charles Christopher Parry, one of the premier field botanists associated with several earlier federally sponsored expeditions (e.g., the Mexican Boundary Survey). The rationale for Parry's abrupt dismissal in 1871 sheds considerable light on the attitudes behind the declining status that descriptive botany and accompanying herbarium specimens had already attained by this time. According to Frederick Watts, Parry's superior as Commissioner of Agriculture, in a letter to Torrey, Gray, Brewer, and D. C. Eaton (reprinted in Gray 1871):

> . . . [N]othing at all had been done by Dr. Parry beyond his attention to the preservation of the herbarium. This Department is designed to render the developments and deductions of science directly available to practice, that farmers and horticulturalists may be benefited by them. The principles of vegetable physiology, their relations to climate, soils, and food of plants, and the diseases of plants, which are principally of fungoid origin, it is clearly the duty of a botanist to investigate. If possible, he should throw some light upon the origin and condition of growth of the lower orders of cryptogamic botany. This is a domain into which I could not discover that Dr. Parry had ever entered, so far as his practical work here gave any indication. The routine operations of a mere herbarium botanist are practically unimportant.

Further prodding by Gray yielded the information that insubordination, at least as perceived by Watts, may have provided the true grounds for dismissal. In any event, Gray's subsequent recommendation helped Vasey get the vacated position, and with 'patient effort' Vasey managed to overcome 'the lack of appreciation of those in high office who thought it a waste of time and money to advance the sciences which wait upon and promote true ag-

riculture' (Canby and Rose 1893, p. 173), and proceeded to build up the collection extensively.

Vasey was joined by Frederick V. Coville in 1888, who was then recruited to participate in a new federally sponsored initiative to survey the biological resources of the nation. Perhaps Coville's inclusion was spurred in part by an 1887 editorial in *Botanical Gazette* (12:197–198), which decried the cessation of federal support for botanical exploration following the coalescence of competing surveys into the USGS: 'Millions have been spent in increasing our knowledge of the other riches of our domain, but the plants have been left to private enterprise . . . a few thousand dollars from an overflowing treasury could be made to yield an ample return in our better knowledge of one of the noblest and (in a public way) most neglected sciences.' As summarized by Coville (1893, p. 1):

In 1886 and subsequent years appropriation was made by Congress for a study of the geographic distribution of animals, to be conducted by the Division of Ornithology and Mammalogy, United States Department of Agriculture. In the year 1890 the scope of the work was enlarged by an act of Congress so as to include the distribution of plants as well as animals, and in accordance with this provision the writer was temporarily detailed from the Division of Botany as botanist of the Death Valley Expedition, the first of the biological surveys under the new act. The work was planned and conducted under the direction of Dr. C. Hart Merriam, chief of the Division of Ornithology and Mammalogy. The botanical work undertaken by the writer was to collect and identify the plants of the region traversed by the expedition, to collate those data which had reference to the range of species, and to arrange this accumulated material in such form that it would be useful in studying the facts and problems of geographic distribution.

Subsequent appropriations were made annually 'for botanical exploration and the collecting of plants in little known districts of America in connection with the U.S. National Herbarium' (Coville 1890), eventually resulting in the first state floras for Washington (Piper 1906), New Mexico (Wooton and Standley 1915), and Nevada and Utah (Tidestrom 1925), among multiple other publications on the botany of North America and other parts of the world. However, initial support for botanical survey, probably minimal at best, appears to have quickly declined, as evidenced in the correspondence of one collector, John B. Leiberg:

During the past three summers I have been fortunate enough to obtain a commission from the Dept. of Agri. for field work in the Columbia basin. As the routes are long, one obtains a pretty good field knowledge of many species over a considerable area. For this reason the position is desirable. From a pecuniary standpoint of view it is not. A commission is only given for a limited period of each year and the expense involved in providing transportation and the details of one's outfit absorb from 50% to 80% of the total salary that the commission carries. . . . Whether these explorations will be continued I do not know. So long as there is any money available for field work there seems no good reason why they should not. . . . A great deal of our territory is so difficult and expensive to explore that unless some Gov't aid is afforded we will never know the complete flora of these regions. Sheep and cattle are rapidly destroying the native plants and by the time private explorations reach these regions the flora will have been totally exterminated by such agencies.

(Leiberg to C. V. Piper, 5 July 1896 [printed in *Sage Notes* (Idaho Native Plant Society) 21(4): pp. 6–7])

Piper, to whom this correspondence was addressed, likewise received minimal support for his efforts, with field work 'carried on in chance hours of leisure and in occasional summer vacations' (Coville in Piper 1906, p. 5).

Leiberg's 1895 instructions represented a shift from general floristic survey to a comprehensive overview of topography, climate, timber resources, and aboriginal uses of native plants (Coville in Leiberg 1897, p. 1). The timber focus was tied to the controversial Forest Reserve Act of 1891, which gave the President authority to establish forest reservations from public domain lands. This act was passed in response to the devastation that was being wrought by unregulated exploitation of western resources, as well detailed in Leiberg's report:

The next and last stage in the destruction of the forests, which is still in active operation, came when the great ore deposits in the Couer d'Alenes [in northern Idaho] were discovered. Thousands of prospectors flocked into the country then, and the forest fires raged in hundreds of localities to clear away the dense growth of timber and shrubs, which very materially interfered with the work of the prospectors seeking mineral-bearing lodes. As the mines began to develop, fuel and timber were needed. The choice parts of the forest were cut into, debris took the place of the green tree, and fire coming later, finished what the axe had spared.

(Leiberg 1897, p. 3)

The resultant Forest Reserves, initially established within the Department of the Interior in 1897, were transferred to the USDA in 1905, and in 1907 were renamed National Forests in order to counter the impression that they had been completely withdrawn from use. The responsible agency was like-

wise renamed, in 1905, from the Bureau of Forestry to the U.S. Forest Service (McClure and Mack 1999).

During this period the Division of Ornithology and Mammalogy, within which botanical surveys associated with the U.S. National Herbarium had been initiated, also went through several metamorphoses, being renamed the Division of Biological Survey in 1896 and, in 1905, the Bureau of Biological Survey. In 1939 it was furthermore transferred from USDA to the Department of the Interior, and the following year consolidated with the Bureau of Fishes to form the U.S. Fish and Wildlife Service. By this time, however, whatever support might have once existed to undertake a comprehensive botanical inventory at the national level had essentially disappeared.

On the other hand, impetus for scattered species-level inventories, at least for a selection of rare species, was triggered with the passage of a diversity of environmental legislation at both federal and state levels (e.g., Endangered Species Act, California Environmental Quality Act), beginning in the late 1960's. One result has been a flurry of species-level surveys done as part of environmental impact statements, often limited to the target species but sometimes more comprehensive, with quality ranging from superb to dubious. As a broad generality with many exceptions, these have largely resulted in unvouchered species lists scattered throughout the 'gray' literature of environmental documentation, or in the file cabinets of governmental agencies and consulting firms. Efforts to compile this massive accumulation of potentially invaluable distributional information have begun (e.g., CalFlora [www.calflora.org]), though the complications in doing so have proven to be daunting. Furthermore, the majority of these surveys have been largely decoupled from the systematics community who formed the core of earlier botanical survey efforts, and who continue to have primary responsibility for the comprehensive synthesis of floristic information. Various limitations and pitfalls resulting from this decoupling are discussed later in this paper.

PAST AND FUTURE ROLE OF THE UNIVERSITY AND JEPSON HERBARIA

The California Geological Survey not only served as a precursor to the USGS and many of the contemporaneous biological survey efforts highlighted in the preceding section, but also set the stage for the long involvement of the University of California at Berkeley (UCB) in botanical surveys of California and the western United States in general. Whitney, as both director of the CGS and chairman for the commission that drafted plans for the future State University (Brewster 1909), claimed that:

[T]he establishment of the Geological Survey was in fact the first step towards the production of a State University. Without the information to be obtained by that Survey, no thorough instruction was possible on this coast, either in geography, geology, or natural history; for the student of these branches requires to be taught in that which is about him, and with which he is brought into daily contact, as well as that which is distant and only theoretically important.

(quoted in Stadtman 1970, p. 27)

Perhaps because of Whitney's influence (and/or for fear that the collections would otherwise remain at Harvard University, which Whitney had been accused of acting for the benefit of [Brewster 1909]), the 1868 Organic Act establishing the University of California specified that:

The collections made by the State Geological Survey shall belong to the University, and the Regents shall, in their plans, have in view the early and secure arrangement of the same for the use of the students of the University, so soon as the geological survey shall be completed, and of giving access to the same to the public at large and to visitors from abroad; and shall in every respect, by acts of courtesy and accommodation, encourage the visits of persons of scientific tastes and acquirements from other portions of the United States and of Europe, to California. The said collections shall be arranged by the resident Professors of the University in a building by themselves, which shall be denominated the 'Museum of the University.'

(California Assembly Bill No. 583, Sect. 24)

Tradition has it that an initial set of CGS botanical specimens was received by the University in 1872, thereby establishing the University Herbarium (in fact if not in name), though no records have been located to confirm this (Ertter 2000b).

In any event, there is evidence that in-house collecting activities began within the first few years of the University's existence, as evidenced in a printed report submitted by Joseph LeConte (1875), hired as the first professor of Geology, Natural History and Botany when the University opened its doors: 'In accordance with my promise I hereby make a brief report of the results of the recent excursion made by the University Scientific Party. The party as you know was organized for the purpose of utilizing the Spring recess of a week, in giving some practical instruction in Geology, Lithology, and Surveying; but expected also to make some collections of plants, rocks, fossils, etc., for the Museum.' The party spent a full week to travel from Berkeley to Black Diamond Mines and Mount Diablo and back: 'As our time was very limited we stopped but little until our objective points were reached.' About 150 plants were collected by 'our young botanist' Franklin P. McLean: 'Whether any of these are new or not remains to be determined.' McLean,

a graduate of the University's College of Pharmacy in 1875, also accompanied LeConte's expedition to Yosemite in the summer of 1875 and collected elsewhere in California, in the process unfortunately assigning the wrong locality to several collections (Jepson notebooks: Calif. Bot. Expl. II: pp. 99, 118–119, 128, 188).

This early collecting tradition received new impetus with the arrival in 1885 of Edward Lee Greene as the first full-time Professor of Botany, assisted by Marshall Avery Howe and attracting such dedicated students as Willis Linn Jepson and Ivar Tidestrom. In 1891, the Chamisso Botanical Club was organized at the University 'by officers and students interested in botanical work. The promoters of the club had especially in view the collection of material upon which to found local plantlists' (Jepson 1894, p. 171). Different members staked out territories, in which trespassing by rivals was discouraged, with one exception: 'Professor Greene as the Great Chief was of course free from all restrictions. We had too much to gain from his friendship to object to his hunting on our grounds' (Frederick Theodore Bioletti, quoted in Ewan 1955, p. 35). Tidestrom would go on to be one of the botanists working for the U.S. National Herbarium, whose efforts resulted in the first flora of Utah and Nevada (Tidestrom 1925). Jepson himself remained at Berkeley, amassing the extensive collection that would ultimately be donated to the University as the core of the Jepson Herbarium (Beidleman 2000). Jepson's personal activities were greatly supplemented by the extensive network he cultivated throughout California, ranging from lawyers to farmers to high-school teachers (Ertter 2000c).

Beyond the extensive collecting activities of faculty, staff, students, and others connected with UCB, which followed these early beginnings, there has been a strong tradition of large-scale collaborative survey efforts with various federal and state land management agencies. The most extensive was the Vegetation Type Mapping Project (VTM), with the U.S. Forest Service acting as lead agency (Wieslander 1935). The concept was purportedly inspired by a course taught by Jepson (Jepson et al. 2000). The original scope of the VTM entailed 220 map units (Wieslander 1935), coinciding with topographic quadrangles, but only 23 were published before further activities were disrupted by the outbreak of World War II (Wieslander et al. 1932–1943). In addition to maps, the VTM resulted in over 23,000 vascular plant collections that are now housed in the University Herbarium:

[The VTM collection] includes many plants in addition to those required for authenticating the maps and sample plots. Very complete field notes accompany each specimen, comprising information as to collector, date, elevation, location, also notes as to size and character of the plant, the slope exposure, the formation in which it grows,

and the names of the more common associated species. The primary purpose of the herbarium is to serve as a check upon field identifications, and to afford a permanent record of the plants collected in each quadrangle. Probably its greatest value, however, will lie in the wealth of material from all parts of the region, and in the detailed information, as to the range, habitat, and associated plants that will be available for each species. (Wieslander 1935, p. 142)

The VTM vouchers have been an invaluable addition to the University Herbarium collections, and have been used as types of at least twelve taxa: *Arctostaphylos glutinosa* B. Schreib., *A. morroensis* Wiesl. & Schreib., *A. otayensis* Wiesl. & Schreib., *A. rudis* Jepson & Wiesl., *A. pilosula* Jepson & Wiesl., *A. silvicola* Jeps. & Wiesl., *Ceanothus otayensis* McMinn, *Galium andrewsii* A. Gray var. *gatense* Dempster, *Githopsis pulchella* Vatke subsp. *campestris* Morin, *Helianthemum suffrutescens* B. Schreib., *Melica californica* Scribn. var. *nevadensis* Boyle, and *Sidalcea hickmanii* Greene subsp. *anomala* C. L. Hitchc. Several of these were described by researchers unconnected to the VTM, long after the survey had ended.

As an apparent offshoot of the VTM, and thereby likewise owing a debt to Jepson, a massive effort to map the vegetation of the Western National Parks was initiated by Harold E. Bailey (H. Bailey and V. Bailey 1941; V. Bailey and H. Bailey 1949). As recalled by his wife and coworker, Virginia Long Bailey:

I met Harold E. Bailey, who had just come up from U.C.L.A., planning to work toward a Ph.D. degree under Lee Bonar. The Ph.D. degree was finally completed in 1935 just prior to the start of the Vegetation Type map Survey of the Western National Parks. During this three-year project (1935–1937, extending into Olympic Nat. Mon. thru 1938 with us) the winter periods were spent in Berkeley and my work with Dr. Jepson was continued part time. . . . I think the summer of 1933 must have been the time that Harold had done some veg. type map work with the Sequoia crew [of the VTM], led by Theodore Plain. (V. Bailey to R. Beidleman, 11–20 May 1996)

Mapping activities were conducted by crews recruited from a variety of sources, with participants often going on to higher level positions within the parks and other agencies. As recalled by John Rutter, former Assistant Superintendent of Rocky Mountain National Park:

I had to quit school to work awhile in 1934. I went to work as a helper in a type map crew for A.E. Wieslander in the California Forest and Range Experiment Station. I was loaned to Yosemite N.P. for 90 days to map much of the Park

north of the Valley. I didn't ever go back to the Forest Service. . . . I knew Harold as a teaching assistant before he became project leader for the type map.

(Rutter to R. Beidleman, 7 November 1996)

Even more than the VTM, the National Park mapping project involved a close collaboration between federal land-management agencies, in this case the U.S. National Park Service, and UCB, taking advantage of depression-relief funding:

The plant collecting activities in which we were involved were in connection with a vegetation type map survey (of the western national parks) carried out under a government sponsored 'Emergency Conservation Works' project under the direction of the western regional office of the Division of Forestry of the National Park Service during a three-year period, 1935–1937. . . . Headquarters was on the University of California campus in Berkeley and an agreement was reached with the University of California herbarium to identify the plant collections. They were to retain a duplicate set of the collections identified and send a list of the identifications to each park area involved. Duplicates should have been left at park headquarters in each case, but if not, then the herbarium was to send a set along with the list of identifications.

(Bailey and Bailey to Wm. M. Lukens, Supt., Chiricahua Nat. Mon., 3 September 1974)

As with the VTM, this productive collaboration was disrupted with the onset of World War II and the end of Emergency Conservation Works funding. Not only was mapping work discontinued, but budget cuts within the University Herbarium precluded further processing of the resultant specimens. Several thousand unidentified, unlabelled, and unmounted specimens languished as backlog until the 1990's, when National Science Foundation funding (BSR-8417804) finally allowed the completion of the University Herbarium's contribution to one of the most exemplary collaborations it has ever been involved in.

One further collaborative survey of California plants took place in the intervening years, involving the UCB Department of Botany, the California Department of Fish and Game, and the U.S. Fish and Wildlife Service. The focus was California's wetland flora, in particular the feeding and resting areas for migratory aquatic birds. Federal funds provided for five year's of intensive field work by a team of assistants working under the direction of Herbert L. Mason, resulting in both the authoritative reference to California's wetland flora (Mason 1957) and thousands of invaluable herbarium specimens deposited in the University Herbarium. This wetland survey, along with the VTM and the Western National Parks mapping effort, serve as exemplary

models for comparable undertakings at a time when accurate information on plant distributions has become increasingly critical.

Isn't It Done Yet? or, You Get What You Pay For

The preceding historical accounts highlight scattered examples of state and federally supported biological surveys that were contemporaneous with the development of the USGS, as well as the involvement of the University of California at Berkeley in such activities. In addition to presenting an overview that has not previously been summarized, this synopsis is intended to emphasize the minimal support allocated to species-level botanical surveys during the period that the USGS topographic mapping effort was in full swing, resulting in the full suite of topographic maps that are now taken for granted. This divergence in support undoubtedly was tied to perceived economic importance, with what botanical component there was increasingly shifted to timber and rangeland resources of immediate and obvious economic significance. As a result, species-level inventories became increasingly dependent on scattered individual efforts outside of any organized framework (Ertter 1995, 2000a).

With the advent of endangered species legislation, however, it suddenly became important to have accurate, comprehensive information on past and present distributions of all plants in the United States. Not only does such information serve as the raw data from which rarity status is initially determined, but it also forms the basis on which informed decision-making depends. The negative consequences of basing critical land-management decisions on incomplete or inaccurate species-level distribution information can cut both ways, increasing the risk of misplaced (and expensive) mitigation efforts as well as the unanticipated extinction of overlooked species (Ertter 2000a). In other words, information that had been treated as primarily of peripheral scientific interest suddenly took on significant socioeconomic importance, over which lawsuits have been fought.

Going beyond rare and endangered species, comprehensive distributional information for all plants is increasingly needed for burgeoning restoration efforts. The importance of such for post-fire restoration is described by Charlet (2000), and information on historical distributions of plants has also played a role in formulating restoration goals for the San Francisco Bay (Goals Project, 1999). On an even grander scale, how much might we depend on comprehensive and reliable baseline information on current plant distributions against which to evaluate the predicted impact of global warming?

Given the current importance of comprehensive botanical inventory and plant distribution information, the question quickly arises: did earlier organized survey efforts, as highlighted previously, sup-

plemented by subsequent scattered efforts, leave us with a legacy of the necessary information? As presented in Ertter (2000a), the answer is a resounding 'No!' Nearly 60 vascular plant taxa per year are still being described from North American north of Mexico, at a remarkably steady rate (Hartman and Nelson 1998). Recent discoveries, many by environmental consultants, range from distinctive shrubs along a well-traveled highway (*Neviusia cliftonii* Shevock, Ertter, & D. W. Taylor [1992]) to a new monotypic genus in the largely agricultural San Joaquin Valley (*Twisselmannia californica* Al-Shehbaz [1999]). Not only is an extrapolated five percent of the national flora yet to be described (Taylor in Ertter 2000a), and therefore subject to extinction from ignorance alone, but the level of distributional information on currently known species is well below that needed for informed decision-making. Charlet's work in Nevada, for example, showed that the distribution of conifers, probably the best-mapped of all plants (e.g., Little 1971), was less well-known than had been assumed, with 40% of the conifer-bearing mountain ranges in Nevada harboring at least one more species than had previously been recorded (Charlet 1996, 2000).

Even where historical distribution has been adequately documented, information on current range is often insufficient to determine rarity status, especially for formerly abundant plants that have lost most of their range to development. The once-common *Horkelia cuneata* Lindley subsp. *puberula* (Greene) Keck, for example, was largely eradicated from the Los Angeles basin before anyone even became aware of its plight (Ertter unpublished data). In the opposite direction, the appearance and spread of non-native plants has been historically under-documented, leading to a massive catch-up effort as the economic impact of invasive species has become evident (e.g., the Sierra Nevada Cooperative Yellow Starthistle Mapping and Assessment Project [Yacoub and Schoenig 2001]). In essence, far from the days of field exploration being well behind us, the need for on-going, organized botanical inventory is both urgent and wide-reaching.

How did the present situation come about, where the gap between available floristic information and what is needed for informed decision-making reached the magnitude it has? Some blame can be laid on the systematics community itself, which has been guilty of seriously underestimating the task and overestimating what had already been accomplished (Ertter 2000a). Whitney's introduction to the botanical report of the California Geological Survey (Brewer et al. 1876) is a prime example: 'The total number of species thus included was estimated at two thousand and it was thought that the work of determining and describing them would not occupy more than a year or two.' As previously noted, the work took considerably more than two

years, and the final tally of 3500 species was nearly twice the original estimate. Even this, however, was only half the number of vascular plants currently recorded from California (Hickman 1993), and the actual number is a matter of speculation. A parallel is readily seen with Powell's underestimation in carrying out his vision of comprehensive topographic mapping, as noted earlier, in the contrast between initial expectations of the task involved with the actual magnitude of effort required.

An even greater determining factor, however, has been the support (or lack thereof) provided for ongoing species-level botanical inventory by society in general and the scientific community in particular, which controls funding, hiring, and promotions based on what is perceived to be a suitably appropriate scientific undertaking. Watts' negative evaluation of Parry's contribution to science, quoted previously, shows how deep-rooted the resistance to botanical inventory is. Paradoxically, my impression is that society-at-large, far from believing that the generation of species-level distributional information is undeserving of institutional support, instead takes for granted that such support has existed all along, fully parallel to the topographic mapping effort of the USGS. The resultant assumption is that comprehensive species-level distribution maps should *already* be available as needed, for all of the above-cited purposes. Instead, as the preceding historical account demonstrates, as a society we've simply gotten what we've paid for.

THE CONTINUING ROLE OF VOUCHER SPECIMENS

To the extent that the desirability of comprehensive, reliable, species-level plant distribution information is acknowledged, two somewhat contradictory stances have been adopted: either that all essential information already exists and simply needs to be compiled (the informatics approach); or that such a goal is completely unrealistic, and that various short-cuts must therefore be pursued (the indicator species, gap analysis, and/or vegetation mapping approaches). These alternate approaches are unquestionably valuable, both for their own sakes and as components of a larger undertaking, but none can sufficiently take the place of a comprehensive species-level inventory involving both voucher specimens and the systematic community. The limitations of vegetation mapping divorced from species-level information are addressed admirably elsewhere in this symposium volume (Charlet 2000). Some limitations of the compilation approach have been elegantly analyzed by D. W. Taylor, mostly as work-in-progress.

A key limitation of the compilation approach is its dependence on the adequacy of existing data sources. Figures 1 and 2, generated by Taylor, illustrate the inadequacy of existing documentation of species-level plant distributions in California, based on herbarium specimens in the University
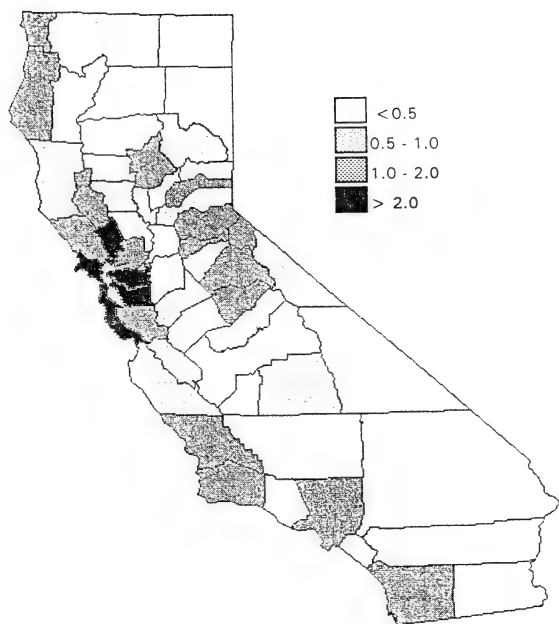
Fig. 1. County map of California showing density distribution of UC/JEPS specimens (sheets/km²), based on a total of over 280,000 sheets.

Fig. 2. Relationship between the collection density of Asteraceae (sheets/km²) and the proportion of Asteraceae county records vouchered. Symbols: ● = counties treated by a local flora; △ = other counties. The line shown was selected from amongst a variety of model forms tested based on overall goodness-of-fit ($R^2 = 0.37$, $P < 0.001$). San Francisco County was excluded from the plot (cf. Fig. 1). (D. W. Taylor, unpublished data).

Herbarium (UC) and Jepson Herbarium (JEPS) at the University of California at Berkeley. Although these collections are obviously only a subset of the total number of herbarium specimens in existence available, they are nevertheless representative enough to serve as the basis for initial rough analyses, as presented here. Figure 1, showing collection density per unit area (averaged throughout a county), illustrates the non-uniformity of documentation coverage among the different counties of California. Some of the non-uniformity can be readily explained (e.g., the highest densities in counties surrounding Berkeley; J. P. Tracy's intense collecting efforts in Humboldt County; exchange from herbaria in various southern counties), but the overall pattern of irregular coverage is irrefutable. Furthermore, evidence from other sources underscores how much remains to be documented even in high-density counties. Recent work on the Mount Diablo flora of Contra Costa County (Bowerman and Ertter in press), for example, increased the previously documented flora (Bowerman 1944) by 26%, over half native. Several fully established non-natives were even additions to *The Jepson Manual* (Hickman 1993): e.g., *Dittrichia graveolens* (L.) Greuter and *Trifolium tomentosum* Willk. ex Nyman. In that the recently collected vouchers for the Mount Diablo study have not yet been accessioned, they represent material beyond that included in Taylor's analysis in which Contra Costa County already has one of the highest collection densities.

Figure 2 carries the California-wide analysis a step further, attempting to correlate collections density of each county (*x* axis) with completeness of species documentation (*y* axis), as calculated by comparing predicted occurrence of species of Asteraceae (extrapolated from multiple sources) against the holdings of UC/JEPS. To the extent that this admittedly preliminary analysis is informative, it may be that only 80% of the vascular plants have been documented from even the most heavily collected counties.

Of course, one question that begs to be addressed is, why limit distribution reports to those documented by herbarium vouchers? There is indeed legitimacy in supplementing documented distributions with unvouchered reports (such as the huge number of species lists resulting from various environmental surveys referred to previously), to the extent that an acceptable level of reliability can be determined. Unfortunately, the limitations of determining reliability without a voucher quickly become apparent, underscored by the frequency with which determinations of vouchered occurrences are changed over time for a variety of reasons. Although some changes result from outright initial misidentification, the majority reflect altered taxonomic circumscriptions as our understanding of species boundaries and relationships improves. Examples of both kinds of changes are represented in

the updated Mount Diablo flora (Bowerman and Ertter in press), verifiable because of the profuse vouchers cited in the original flora (Bowerman 1944). Both voucher specimens for *Prunus emarginata* (Hook.) Walp. in the 1944 edition, for example, have been reidentified as escaped cultivated species, so *P. emarginata* has been eliminated from the more recent edition. Alternatively, vouchered references in the 1944 edition to *Oenothera hirtella* var. *jonesii,* which had subsequently been split among several taxa (Raven 1969), could be updated to the correct taxa as now circumscribed, something that could not be done with unvouchered citations.

Echoing Wieslander's previously quoted comments on the VTM collections, as well as arguments by Goldblatt et al. (1992) and Ferren et al. (1995), the importance of voucher specimens was clearly emphasized in the report, *A Biological Survey for the Nation,* prepared by the National Research Council of the National Science Foundation (1993, p. 68):

> Collections of specimens are a critical component of the [National Partnership for Biological Survey]. In all but a few well-known taxa, identifications of species must be based on voucher specimens, without which frequent misidentifications are certain to be made. Faulty management decisions are likely to result from incorrect identifications. Collections are repositories for most of what we know about species diversity and are constantly pressed into use for new and often unexpected purposes.

The critical role played by vouchered documentation of species-level distributions, and the limitations of the purely compilation approach to distributional information, is further emphasized when the extent of rejected reports is realized. Although the value of indicating excluded species (i.e., taxa that at one time or another had been included within the group but which are now treated as members of other groups) is well-established in monographic works, the need for comparable lists of excluded or rejected species in floristic works has not generally been appreciated. This has not been a significant problem in monographic floristics, which largely rely on voucher specimens, other than increasing the likelihood of redundant effort anytime the source of the excluded report resurfaces. Keeping track of erroneous or dubious reports becomes critical, however, now that mass compilation of species-level distribution reports from multiple sources has become popular. The magnitude of the potential error can be seen in some floristic examples that have attempted to indicate rejected reports; e.g., 97 in the East Bay flora (Ertter 1997), 66 in the Mount Diablo flora (Bowerman and Ertter in press), equivalent to 6% and 8% respectively of accepted taxa in each flora. Excluded reports include misapplications, confirmed misidentifications, and vouchers

with suspect localities, but mostly represent unvouchered reports of dubious nature, often far outside known distributions. Although it has been insufficiently acknowledged, critical evaluation and decision to exclude reported occurrences has in fact been among the primary responsibilities and contributions of the systematics community to species-level distributional informatics.

'ORGANIZED' FLORISTICS AND THE SYSTEMATICS COMMUNITY

The significance of critical evaluation by the systematics community stands as a key distinction between the compilation approach to biodiversity informatics, whether electronic or printed, and that employed in established floristics, in which the contents are carefully evaluated, filtered, and synthesized. This distinction underlies Jepson's characterization of compiled, accreted, and organized floristic works, expressed in a recently unearthed letter to Wieslander (3 April 1939, JEPS archives):

> There are three kinds of manuals. First, a manual that is compiled. Second, a manual that is accreted. Third, a manual that is organized. A compiled manual, for example, is such as Coulter's [1885] Manual of the Rocky Mountain Flora (not Nelson's [Coulter and Nelson 1909], but Coulter's). Taken wholly from the literature, nothing is left out, nothing omitted. It is philosophically speaking, perfect and complete. But no real botanist, I think, ever looked within its pages. It is to him useless. . . . Then there is the manual that is accreted. In this case everything is put in, not only from books but also from plants. It, too, leaves nothing out. It adds everything that comes along, both from plants and the literature. It is, also, philosophically speaking, perfect and complete. And, finally, there is the Manual that is organized. My Manual of Botany [Jepson 1923–1925] is organized. It is not perfect nor complete, nor can ever be in a thousand years. The whole treatise is, however, organized into a single unit, every part depending and related and associated with every other part. And it is made up basically from research on plants.'

Jepson's concept of an 'organized' floristic work, with 'every part depending and related and associated with every other part,' is equivalent to the argument in Ertter (2000a) that floras and other kinds of taxonomic treatments are best understood as complex models, encompassing multiple units whose exact identities depend on their relation to other units within the larger context. A prime example is provided by Fig. 3, contrasting four alternate taxonomic models that had been developed to circumscribe taxa within the *Juncus triformis* complex. Although this type of situation has sometimes been disparaged as evidence of the systematic community's purported inability to agree on standards,

COMPARATIVE MODELS OF JUNCUS TRIFORMIS COMPLEX

pre-Hermann	Hermann, 1948	Cronquist, 1977	Ertter, 1986
J. triformis var. stylosus	J. triformis	(not addressed)	J. triformis
	J. megaspermus		
	J. leiospermus		J. leiospermus var. leiospermus var. ahartii
J. triformis var. brachystylus	J. kelloggii		J. kelloggii J. luciensis J. tiehmii
	J. capillaris		J. capillaris
J. triformis var. uniflorus	J. bryoides	J. kelloggii	J. bryoides
	J. uncialis		J. uncialis
	J. hemindytus		J. hemidentyus var. hemiendytus
	J. abjectus		var. abjectus

FIG. 3. Comparison of four taxonomic models (monographic treatments) of the *Juncus triformis* complex. Note in particular the dramatically different circumscriptions of *J. kelloggii* between models.

it is actually a straight-forward case of science in action, with earlier hypotheses and models giving way to new ones in the face of additional evidence. In this particular example, Cronquist (1977) hypothesized that the series of species proposed by Hermann (1948) did not meet the accepted criteria for recognition as distinct species, but rather 'appear to be mere technical variants, often locally constant as in self-pollinated groups in other genera, but with widely overlapping ranges and similar habitat requirements.' In that Cronquist himself was aware of the limited evidence on which his model was based, he encouraged one of his students to put it to the test and was fully accepting of the alternate model that resulted (Ertter 1986), which was based on five years of focused field work, common garden studies, chromosome counts, and seed coat micromorphology. The importance of this particular example in the present context is to illustrate the pitfalls associated with attempts to deal with taxonomic units as free-standing entities divorced from a specific model, as is generally the case in mass compilations. For better or worse, the nomenclatural system adopted by the international systematics community ties the name to a type specimen, not to a circumscription. As a result, the binomial *Juncus kelloggii* Engelm., rather than serving as a unique identifier, can code for three very different entities, depending on whether it is in the context of Hermann's, Cronquist's, or Ertter's model. Compilation efforts that are unable to take this into consideration will inevitably end up generating the most inclusive circumscription (e.g., that of Cronquist) even if this is not the currently accepted circumscription. This can be seen, for example, in the distribution map generated for *J. kelloggii* in the

PLANTS database (http://plants.usda.gov:80/plants/), which shows a range significantly larger than the documented range published in 1986.

Another example illustrating the nature of an 'organized' taxonomic work is provided by the recent description of *Deinandra bacigalupii* B. G. Baldwin (1999b), based on what had previously been treated as a disjunct northern population of *Hemizonia increscens* (D. D. Keck) Tanowitz subsp. *increscens* (e.g., Tanowitz 1982). Not only did publication of this new species provide impetus for Baldwin to publish his emerging generic realignment of tarweeds that had resulted from morphological and molecular phylogenetic analysis (Baldwin 1999a), but publication of *D. bacigalupii* also created a new circumscription of *Hemizonia/Deinandra increscens*. As a result, *D. bacigalupii* cannot simply be added to existing floristic treatments (e.g., Hickman 1993) without simultaneously modifying the description and distribution of *D. increscens* to reflect its reduced circumscription.

The purpose of the preceding paragraphs is to clarify that critical analysis by members of the systematics community, rather than being peripheral, is an essential component of on-going botanical inventory. This is by no means intended to downplay the equally critical involvement of agency biologists, environmental consultants, and avocational enthusiasts, who are in fact currently responsible for generating the bulk of new field-gathered information (Ertter 1995, 2000a). The point is that our modeling of biodiversity is still very much a work-in-progress, such that even the seemingly mundane aspects of plant distribution information are often clues to the undescribed 5% of the North American flora, or to the 'cryptic' diversity that is also a crit-

ical component of biodiversity (Baldwin 2000). As one example, the revision of the Mount Diablo flora (Bowerman and Ertter in press), as localized as it was, nevertheless involved numerous interactions with taxonomic specialists to address discrepancies between local variation (i.e., plants that 'hadn't read the book') and treatments in *The Jepson Manual* (Hickman 1993), often resulting in changes to the latter. This is in part what Jepson (cited above) meant by a flora 'organized into a single unit, every part depending and related and associated with every other part,' and what he expanded on in the same letter:

One of my students opened a bundle of plants [in my collection] and exclaimed: 'Why, Dr. Jepson, here are species new to California from the eastern Mohave borders collected by yourself. Why did you not put them in the Manual?' I had to explain that these were critical species which would have taken a long time to determine; and, even after determination, would require a long time for organization into the manuscript. It was not possible to delay the Manual further. In his inexperience the student imagined species could be added just like adding another stick to a pile of cordwood. He had no conception of the hundreds of comparisons involving detailed analysis that must be made in the case of every species added to a systematic account. Even botanists in general have no notion of the mass of work involved in a large systematic treatise.

LOOKING AHEAD: THE HARVEST TO COME

Given the preceding discussion on the historical and current status of species-level botanical inventory in the United States, it is evident that most of the perceived obstacles to on-going efforts are based on false assumptions. Instead:

- The results of such efforts have significant pragmatic implication and potential economic impact, primarily as a critical component of informed land-management decision-making. As a result, properly done survey efforts prove their worth in the long run and have even received significant support from far-sighted private donors on that account (e.g., Stanford's support of the California Geological Survey).
- Federal- and state-funded survey efforts were terminated by politics, special interests, and misconceptions, not because the scientific goals were completed or unimportant.
- The essential fieldwork and critical taxonomic evaluations therefore remain far from finished, and can by no means be offset by simple compilation of existing data, even within a modern informatics framework.

- Herbarium vouchers remain an integral part of scientific documentation, with many more needed to document species-level distributions comprehensively and reliably.
- On-going involvement of the systematics community is likewise integral, not only to address the numerous undescribed species (an estimated 5% of the North American vascular flora) but to ensure that the resultant informatics framework is fully 'organized.'

This leaves the following two assumptions:

- Species-level inventory within the United States is not sufficiently scientific, innovative, or otherwise high-profile to merit funding.
- Comprehensive species-level inventory is simply too big a project to tackle (hence the short-cuts of vegetation mapping, gap analysis, indicator species, umbrella species, etc.)

The first assumption appears to be deeply rooted, at least within the American academic community, such that floristic work has long since fallen out of favor as a suitable topic for graduate work, in spite of Jepson's lifelong efforts to develop floristics as sound science. In Europe, on the other hand, an entire field of chorology has developed around a Committee for Mapping the Flora of Europe, given a recent boost by advances in electronic approaches (e.g., Lahti and Lampinen 1999). This touches on the irony of the exploding prestige and popularity of geographic information systems, often taking place at the same institutions that scorn floristic work by systematists. Most efforts (and funds) to develop essential plant distribution information layers, however, are completely decoupled from the systematics community, relying instead on compilation approaches, with the resultant pitfalls and shortcomings that have been discussed.

Of course, biodiversity informatics as a whole is a favored topic, including within the systematics community itself, spawning a veritable alphabet soup of acronyms at state, federal, and international levels (e.g., as highlighted in ASC Newsletter 28[5], October 2000). At present, however, support for these efforts has been largely directed thus far to massive compilations, perhaps in fact the realistic and appropriate starting points in an absolutely essential and long-overdue undertaking. Existing projects nevertheless appear to be a far cry from fully involving and providing the concomitant support for the systematics community at large, consisting of the multitude of field collectors and monographers who generate the raw data, critically evaluate the results, and synthesize the taxonomic models on which bioinformatics depends.

Complementing such umbrella approaches to bioinformatics, there are a diversity of innovative

approaches that could be capitalized on to increase the availability and reliability of new species-level plant distribution data. Charlet (2000), for example, argues for the coupling of documented species-level information with vegetation mapping. One also wonders how far various funds currently being allocated for studies on individually targeted rare or invasive species could go towards comprehensive mapping of all plant species in an area, minimizing the need for redundant surveys over the same ground when yet one more species becomes of interest. A parallel exists with Jepson's advice to Wieslander to expand his proposed mapping effort beyond economically important woody species, on the grounds that 'New economic aspects developed so rapidly that it was proven repeatedly that an economic map was and must be from its nature transient and insufficient' (Jepson et al. 2000). If this advice had been followed from the beginning, a 'considerable appropriation' could have been saved that was subsequently needed to re-map much of the area already covered.

Tapping into the private sector, Ferren et al. (1995) note that the bulk of undocumented (and under-reported) field observations in the United States currently result from legally required environmental assessments prior to development. However:

> Without vouchers deposited in institutional herbaria, the scientific and even legal credibility of these reports is suspect at best, and their long-term value is minimal in spite of the large sums of money spent in producing the documents. In southern California, it is not uncommon for approximately $1 million to be spent for a specific plan and associated [environmental impact review] for larger development projects. . . . For a little extra money, a much more worthwhile review effort could be undertaken. A client's money would be more wisely spent if vouchers were collected and deposited in a formal herbarium than if the environmental review was not documented professionally . . . since the overall budgets for environmental review studies and documents are substantial, it would take only a modest addition to the budget to cover the costs of collecting and depositing voucher specimens.
>
> (pp. 198, 202)

Beyond and above these and other innovative ways to increase support for on-going botanical inventory, the most fundamental requirement is a change in our understanding of the situation. Rather than being intimidated by the scope of the challenge, I propose that we have not been thinking big enough! We do not have to justify the initiation of a Big Science project; rather, we need to acknowledge that this is exactly what the systematics community has been doing for the last 250 years: a massive international collaboration to model spe-cies-level biodiversity, including distribution, that will remain a work-in-progress for decades, perhaps centuries, to come. We are in this for the long run; the challenge now is to assemble the scattered pieces together in a new collaborative framework, combining the best of the systematics and informatics communities, governmental agencies, conservation organizations, avocational enthusiasts, and private landowners, all within a coordinated, mutually profitable, scientifically valid framework.

If this seems daunting, recall again the seemingly impossible challenge faced by Powell in getting the USGS off the ground, and its subsequent vindication beyond his wildest dreams. In his 1886 defense of the USGS (quoted in Stegner 1953, p. 289), Powell provided this stirring testimony:

> If the work thus begun can be continued through the labors of this Commission, and all of the scientific operations of the Government placed under efficient and proper control, scientific research will be established in America upon such a basis that the best and greatest results will accrue there from. The harvest that comes from well-directed and thorough scientific research has no fleeting value, but abides through the years, as the greatest agency for the welfare of mankind.

What would we have now if a true biological survey had existed parallel to the USGS for the last hundred years? What might the next hundred years' harvest be?

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FLORISTIC STUDIES IN CONTEMPORARY BOTANY

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Abstract

This paper outlines the traditional procedures for monographic and floristic studies, and points out that floristic studies are a link between the producers and the consumers of botanical information.

This paper is derived from a talk titled "Systematics, Informatics, and Floristics" that was presented at the Jepson 50th Anniversary Celebration and Scientific Symposium in June, 2000, at the University of California, Berkeley. The purpose of this paper is to review how botanical information flows from creators to consumers, and the central role of floristics in that process.

Mankind's age-long study of plants has produced an amazing legacy, which is evident in any scholarly library (Barkley 1993). Systematists who add to the accumulating knowledge believe that it all has meaning, and presumably it is useful to people outside of the bounds of botany. The diagrams presented here show how the information of systematic botany is accumulated and how it reaches the consumer in useful form.

Monographs and revisions (i.e., "monography") are the "soul of systematics," as pointed out so neatly by Stuessy (1975). Those studies are taken to be the fundamental syntheses of systematic knowledge and are the roadmaps for subsequent studies. The term "monograph" has been used for the larger and more sumptuous studies, while "revision" has meant studies presented in less detail. The central goals of both are similar, however, and, as with many species, there is no sharp distinction between the two. In this paper, all such studies are called "monographs." Traditional monographs focus on some natural group, such as a genus or a section of a genus, and they include, among other things, delimitations and descriptions of the entities, keys, hard data on ranges and habitats, and an ordered nomenclature. Modern monographs are also expected to include information on the biology of the group and on natural relationships. A how-to outline for a monographic study was presented by A. S. Hitchcock, the noted agrostologist, in a remarkable book called *Descriptive Systematic Botany* (Hitchcock 1925). The book is the product of an earlier era, and even though the author had few of the techniques that are available to us now, it is still well worth revisiting, for the author laid out a clear recipe for the standard procedures of monography. Arguably, contemporary monography rests upon the procedures outlined by Hitchcock, to which have been added many new sources of information and schemes for interpretation.

Two matters were particularly important in the first half of the 20th century for the development of monography. The first was the intentional incorporation of evolutionary questions. Beginning about 1930, a monograph was regarded as incomplete if it did not offer some understanding of evolutionary relationships among the entities under consideration. One of the first and clearest monographs to be published in the USA that had evolutionary relationships as a chief goal was the treatment of the genus *Haplopappus* by H. M. Hall (1928). Therein the author tried mightily to develop phylogenies as he understood them. It is not important that Hall's techniques are now seen as inadequate and that many of the monograph's conclusions are no longer tenable; what is important is that he acted upon the assumption that good monography must be centered upon evolutionary relationships.

The second matter was the advent of new laboratory techniques, which boosted systematic studies into an experimental science with garden and greenhouse studies, cytogenetics, comparative cytology, the analysis of secondary metabolites, etc. These studies came to be called "biosystematics" and have produced imaginative and detailed monographic treatments. Biosystematics coupled comfortably with ecological studies such as pollination, seed dispersal, population biology, and geohistory, thereby further enriching the content of monography.

A new vista in monography was introduced with the arrival of cladistic theory and new information from molecular studies. Cladistic theory supplied a workable tool for showing evolutionary relationships, resulting in phylogenetic trees that could be objectively tested. Molecular studies have proved to be particularly compatible to cladistic analyses, and the two have created a vital subset of systematic studies that focuses on evolutionary relationships, rather than on species delimitation. There is a rich literature on cladistic theory and derived phylogenies. The application of the phylogenetic approach based upon cladistics is comfortably treated

in the recent textbook *Plant Systematics: A Phylogenetic Approach* by Judd et al. (1999).

Contemporary phylogenetic studies have recognized that the traditional Linnaean concept of species is imprecise at best and may be no longer justifiable (i.e., species are indeed specious). From the early 1990's to the present there has been a shower of literature on the creation of a new taxonomic scheme to reflect phylogenetic relationships, and indeed there was a symposium on the topic at the XVI International Botanical Congress in St. Louis, MO in 1999 (cf. Cantino 2000, and Cantino et al. 1999, for an introduction into the literature). It is doubtless true that changes are coming in how we conceive of "species," but the proposed phylogenetic classifications are yet to be elaborated, and are yet to be taken into the thinking of the consumers of botanical information. For the present, a conservative approach is prudent, and so the treatment of floristic botany rests upon the standard, albeit flawed, Linnaean notions of species.

Floristic studies account for all of the plants that occur in a particular region. Usually this is taken to mean the vascular plants, although the currently active Flora of North America project also includes the bryophytes. Hitchcock (1925) also includes a discussion on the methods of floristics, but without the notion of floras as encompassing summaries. The products of floristic studies are floras or manuals. The two are similar and intergradant, but as with monographs and revisions, the former are more sumptuous, often in several volumes, while the latter are stripped-down for convenient use. Floristic botanists derive their information from monographs and revisions, but when no monographic studies have been done, they must prepare noncetreatments with the information at hand. If a floristic program required that all groups be treated at equal levels of sophistication, the flora would never be written.

Floristics are best done by botanists with field-familiarity in their region who also have good herbarium and library resources. The techniques for synthesis have been largely intuitive, based upon the botanist's memory and ability to organize great amounts of detail. But, just as cladistics and molecular data added a huge new approach to monography, electronic information management ("informatics") is changing floristics. It is now thinkable that a floristic project can account for vast amounts of information that effectively lie fallow, and that, through floristic programs and their computer links, this buried information can be brought to the surface. To be certain, floristic projects that are based on informatic techniques are in their infancy, but the future impact is already evident. Three notable computer-based programs come to mind (but there are others, not mentioned here): (1) The magnificent summary of information on the North American Flora as compiled by John Kartesz in his Biota of North America Program (BONAP) and distributed on a CD-ROM that was prepared by Kartesz and Meacham (1999). (2) The detailed Flora of Florida project centered at the University of South Florida and prepared by Richard P. Wunderlin and assisted by Bruce F. Hansen (a manual was published in 1998). (3) The theoretical works of Hugh Wilson at Texas A&M University. The application of informatics technologies to floristic projects is not easy. The Flora of North America made an effort to incorporate informatics theory, which proved to be administratively difficult.

EXPLANATIONS OF THE FIGURES

Figure 1 simply notes the cascade of information from monographs and revisions through the floras and on to the consumers. The consumers are a mixed lot; here they are called "primary," "indirect," and "ultimate." The primary consumers are scientific and academic professionals whose expertise is not in systematic botany but whose experience gives them the ability to judge the accuracy of the information. These are the botanists' colleagues. The indirect consumers are a large group who use what is in floristic treatments essentially on faith. It is this group for whom the accumulated wisdom in the herbaria and libraries is likely to be of greatest interest and least accessible. Floristic projects have an awesome opportunity to connect this group with botanical information. The ultimate consumer is simply the person who needs information about a plant, e.g., the person who asks, "Is this crabgrass in my lawn? What do I do about it?" In many states, the Cooperative Extension Services are geared to accumulating information from primary consumers and delivering it to the ultimate consumer.

Figure 2 summarizes the preparation of a monograph, starting with the definition of the problem and the early survey work. Items 3 and 4 are critical, for here the monographer's experience (or if a graduate student, the experience of the student's mentor) calls for the building of hypotheses and expressing them as testable models. Items 5–8 are the chief sources of information useful in monography; they are not mutually exclusive, and some techniques have elements of two or more of these items. Clearly, comparative morphology is of great importance because it is easily accessed in the herbarium, there is a lot of it, and the techniques for using morphological information are of long tradition. Items 6 and 8 include such matters as pollination studies, populational studies, introgression, the role of climate change, etc. The last item has become increasingly significant with the advent of readily accessible Geographic Information Systems (GIS). Item 9 is legalistic, mechanical, and utterly essential, for it is how the entities are given their correct names. Information from items 5–8 are assimilated and the results are compared to the hypotheses and models generated in items 3 and 4.

The Cascade of Systematics

1.   **Monographs and Revisions**

2.   **Floras and Manuals about the Plants of a Region**

3.   **Primary Consumers: e.g., Ecology, Agronomy, Forestry,
      Conservation Biology, Geography, Pharmacology, History**

4.   **Indirect Consumers: Popular Works, e.g.,
      Books on Wildflowers, Natural History, Trees, Weeds**

5.   **The Ultimate Consumers
              "The Person on the Street"**
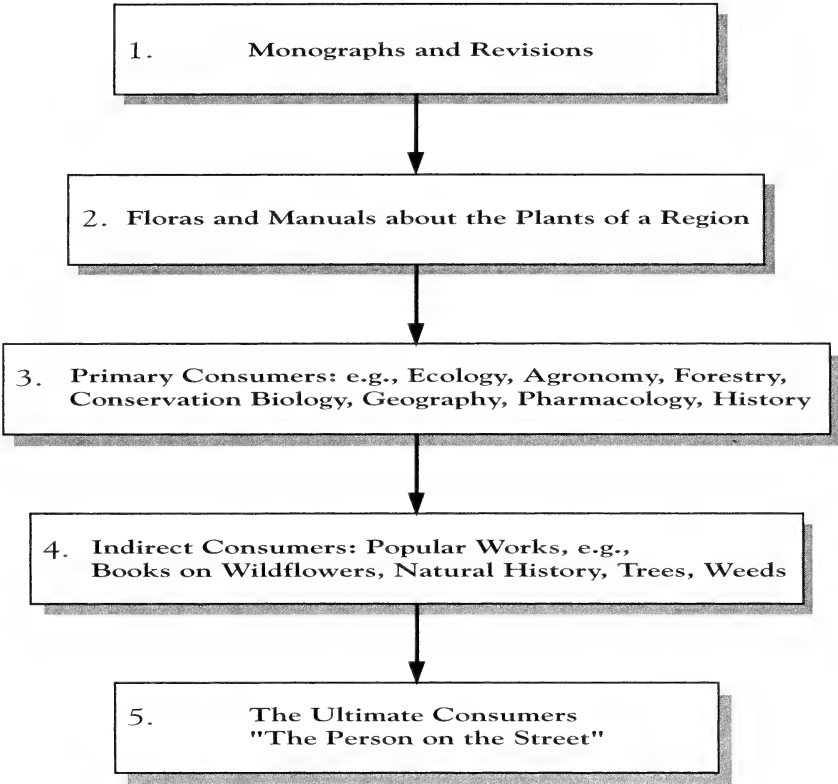
FIG. 1.   Explanation in text.

During the assimilation stage, phylogenetic (cladistic) techniques are applied, which yield justified evolutionary trees showing the current understanding of natural relationships. It is noteworthy that many phylogenetic studies that are based on molecular data focus on higher groups, such as genera or families, and that species-centered phylogenetic studies often rest upon large components of morphological data. Item 12, integration, is the aligning of the information into the customary format for monographic studies. Keys, descriptions, specimen citations, sources of data, and conclusions drawn are presented in traditional ways, making the monograph (item 13) a readily understandable and useable document, whether published as hard copy or on a website.

Figure 3 notes the assimilation of information from monographs and other sources into a floristic treatment. Items 1 and 2 are obvious; the parameters of the project must be understood to account for the biological complexities of the region and the expectations of the intended users of the flora. Primary information is taken from monographs and revisions as much as possible, but when no monographic works are at hand, it is necessary to create treatments as best as possible; this step essentially incorporates items 3, 4, and 9 of Figure 2. Item 4, preparation of the treatments, is demanding and most easily accomplished by botanists with at least some monographic experience. Computer-assisted techniques are potentially very useful in item 4 (e.g., DELTA) but to date these techniques have long and steep learning curves. Many floristic botanists are not ready to embrace the computer as a tool to prepare keys, descriptions, and other textual matters. However, computer-based programs for generating maps are clearly with us. Text matters generated in item 4 can be entered into a website

Preparation of a Monograph or Revision

1. Definition of Problem
2. Herbarium, Library, Field Surveys
3. Eyeball Materials to Build Hypotheses
4. Tentative Taxonomy and Biological Models
5. Comparative Morphology and Geography (Herbarium)
6. Breeding and Behavioral Studies, "Biosystematics" (Field and Garden)
7. Cytological, Biochemical, Anatomical and Molecular Studies (Laboratory)
8. Biogeography and Geohistory (Library and Field)
9. Nomenclature
10. Phylogenetic Analyses
11. Assimilation
12. Integration
13. Systematic Monograph or Revision with Phylogenetic Interpretation

FIG. 2. Explanation in text.

to facilitate the following steps and the production of the final flora. Item 6 is also particularly demanding, for here is where the tentative product is critically tested and edited for accuracy. Taxonomic reviews treat the botanical matters; regional reviews account for distributions and regional variation. Item 7, amplifications, is the addition of information needed by the intended users of the flora, i.e., the consumers. Item 8 is where the manuscript is treated for editorial consistency, where the general keys are created and tested, and where the introductory essays are prepared and incorporated. The product may be published as hard copy (item 10) or posted on a website (item 11). A flora that is conveniently available on a website is easy for a primary consumer to consult when addressing broad questions (item 12), e.g., questions that were

not in the minds of the botanists who did the various studies that led to monographs or floras. A flora has a wealth of information relevant to distributions, variations, phenologies, etc., that may be coupled with soil types, geohistorical matters, archaeology, medicine, and other areas not yet conceived. The point is that the hard data of the core of systematic botany are translated for use by others through floras.

CONCLUSIONS

The abiding points are simple: There is a huge body of literature in libraries and specimens in herbaria that are the products of botanical enterprise. Monographic studies are done to determine what entities exist, how to distinguish among them, how

Preparation of a Flora or Manual
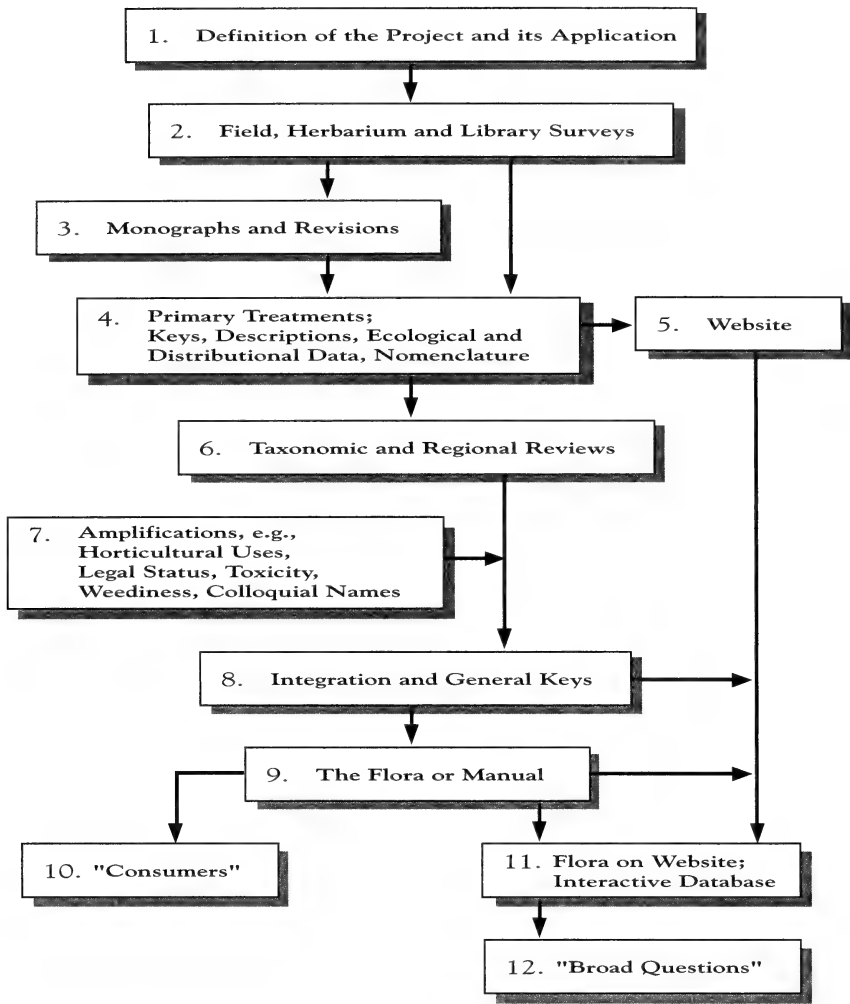
FIG. 3. Explanation in text.

they are related to each other, and how they behave. Monographic studies have spawned very interesting derivatives that relate to sophisticated understandings of evolution, but that still fall within the shadow of monographic studies. Floristic studies filter and assimilate the accumulated wisdom of the plants of a region and couple it to those who use the information. It is not for nothing that we recall a botanical beatitude attributed to the late Lloyd H. Shinners: "Blessed be those who write floras, for they shall discharge the botanists' responsibilities to the public."

Note: A review of the growth of taxonomic concepts over the past half-century was recently published by P. F. Stevens in a series of "Jubilee Papers" in the journal Taxon (Stevens 2000). It appeared too late to impact the presentation of this paper at the Jepson Symposium in June, 2000.

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COUPLING SPECIES-LEVEL INVENTORIES WITH VEGETATION MAPPING

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ABSTRACT

The importance of high quality vegetation maps for land management is rapidly gaining recognition. Unfortunately, most vegetation maps in the western USA are old, have coarse resolution, or are not ground-truthed. Vouchers for these maps, even of the dominant species, are lacking. This makes natural resource management decisions, including those made during disasters such as fire, difficult or sometimes damaging because managers lack the basic information they need to make these decisions. In an effort to fill the information gaps, many vegetation mapping projects have been implemented across the nation, but those that want the maps often do not think of including species inventories in the mapping activities. At the same time, botanists continue to have difficulty finding funding for complete species inventories. This situation represents an opportunity to combine the skills of botanists with the needs of land managers. I present examples of vegetation projects I was involved in, in which I convinced the project leaders to incorporate plant species inventories in the mapping activities. The addition of species distribution information increased the quality, usefulness, and accuracy of these projects. Funding for species inventories can be found in restoration budgets. Botanists should take it upon themselves to involve themselves in mapping projects. Further, if botanists are willing to make their case, they should be able to convince the public and funding authorities to spend a little restoration money on species surveys before the need to restore arises.

It remains extremely difficult to obtain funding for floristic surveys in the United States. This is true in spite of a steady, high rate of new plant species discovery for the past 100 years in California alone (D. W. Taylor in Ertter 2000). Remarkably, most floristic work is performed *pro bono* by both professionals and amateur enthusiasts (Ertter 2000). However, this situation is far from ideal and seriously slows the work. As botanists interested in plant distribution patterns, we know that our knowledge is far from complete. To increase our knowledge of these distributions at the necessary pace, funding must support species inventories. Therefore, we must be creative about how we present proposals to do this work.

We need to learn how to convince management and funding agencies that species inventories are beneficial; not only inventories of vulnerable species, but also of the dominant, common, and uncommon species. We can seize opportunities to further this goal by finding vegetation projects in our area and presenting to project leaders reasons why making voucher collections will improve the project's usefulness. I here present examples from my experience of different situations where species inventories were included in, and improved the quality of, other projects.

VEGETATION MAPS

A vegetation map was probably the first graphic display of plant distributions. Vegetation maps originated with the military in order to provide basic information concerning the structure of vegetation pertinent to the movement of troops, maintenance of supply lines, cover, and other logistical concerns (Küchler 1967). In the western USA, the first wave of vegetation maps were made for the purpose of resource extraction, beginning with Merriam's life zones map (Merriam 1898). Through the 1950's, most of the nation's vegetation maps were economic, a trend that Jepson resisted for decades (2001).

Other important uses of vegetation maps began to emerge into the national arena in 1993 when the Gap Analysis Program (GAP) (Scott et al. 1993) was launched as a national project (Scott and Jennings 1997). However, plant species distributions are only rarely integrated into modern vegetation maps, in spite of rapidly developing Geographic Information System (GIS) technology. Even the GAP project concerns itself mainly with dominant plant species in order to predict the distribution of wildlife habitat (Scott et al. 1993), and species-specific distribution data are usually restricted to vulnerable species. Further, because of growing concerns about climate change, the abandonment of species-level surveys is considered prudent and these are being replaced by "plant functional type" classifications (Smith et al. 1997).

Today, most agency scientists know they need vegetation maps to serve as baseline data to manage public lands. These maps must provide both ecosystem level and species-specific information. One layer should include structural information, that is, the distribution of the kinds (e.g., needleleaf evergreen, broadleaf deciduous) of forests, woodlands, shrublands, grasslands, and riparian systems that occur on landscapes and in regions. Physiognomic and structural information is needed to man-

age for vital ecosystem functions (Küchler 1967; Smith et al. 1997) upon which we depend. This information is also essential when planning for wildlife, recreation, and emergency procedures during natural disasters such as fire and flood. In addition to managing for wildlife habitat and vulnerable species, accurate vegetation maps with species-specific data are needed to plan and conduct restoration projects, and to permit and monitor commercial activities. It is difficult to assign a dollar value to species-level surveys because they produce irreplaceable basic information. However, many existing vegetation maps are fraught with problems, even at the structural, functional level.

Technical aspects. Many of the most utilized maps are old (e.g., Wieslander 1940) or have coarse spatial resolution (e.g., Küchler 1964). Most modern maps lack ground-truthing, have little species distribution data, and only a few recent maps have vouchers. Our vegetation maps need this species-specific distribution data and ground-truthing. We can easily correct all these deficiencies at one time with some planning and a modest budget.

Tying the species information to the vegetation map is easiest when the vegetation classes on the map are delimited by polygons in a GIS. I use the term polygon here to mean an irregular shape on a map with a sharp boundary that corresponds to an area on the ground of relatively homogeneous vegetation (whose boundary on the ground is rarely so sharp). Polygon-based mapping allows for a species-level inventory and the collection of vouchers during the ground-truthing phase of map production because collections and observations can be made within and recorded for individual polygons. The polygons can be identified from aerial photography, as I did (Charlet 2000) by using the methods of Küchler (1967), or from satellite imagery as Hogg et al. (1999) did by using the image segmentation approach of Ma et al. (2001). Once the polygons are in digital form, it is a simple matter to include species data in the attribute table when the voucher location data are precisely recorded. In this way, each polygon gets a species list. The hardest part of these surveys and mapping activities on the ground is actually getting to the sites. Once there, it is a simple matter of making voucher collections and adhering to strict record keeping standards, such as those recommended by Ferren et al. (1995). Species-specific distributions are easy to add to a polygon-based GIS map, even after the map is complete, by simply adding these distributions to the attribute table.

SPECIES INVENTORIES CONCURRENT WITH OTHER PROJECTS

Nevada wildlife map. In 1993, a research group at the University of Nevada was mapping wildlife habitat in Nevada. Since I spent much time in Nevada's outback while conducting my Master's and Ph.D. research, this group approached me to fill in the details concerning the distribution of trees throughout the state and to make a vegetation map of the state. I set about to construct a 1:1,000,000 scale map of the eight vegetation zones of Billings (1951) for Nevada.

In mapping the vegetation of Nevada, I included the distribution of the different conifer species and mapped their occurrences. It was easy to collect vouchers after going to the trouble of getting to and climbing these mountains, and so I did. Once the time allotted for field work was complete and I looked at my list of collections, it appeared that I had more than 100 cases of species in mountain ranges not accounted for in the literature (e.g., Little 1971).

I was troubled by this result, and wondered how many of my "range extensions" were in herbaria but had not been compiled. I went to 15 western herbaria with large Nevada collections, and found even more conifer distributions that were neither mapped by Little (1971) or Griffin and Critchfield (1972), nor used in previous analyses (e.g., Wells 1983). The changes were significant enough to warrant a new analysis, the results of which demanded strikingly different conclusions (Charlet 1995). Careful scrutiny of my collections led to other discoveries, such as extensive gene flow between several juniper taxa in the region (Terry et al. 2000).

Further, since publication of my conifer data for Nevada (Charlet 1996), others and I have found 6 new county records for 4 species, and 12 new range extensions. Altogether, information regarding the distribution of 8 of these 22 species and 9 different mountain range conifer floras have changed since 1996. There are more than 4000 vascular plant species in the Great Basin/Mojave Desert region, but Nevada's conifers represent less than 0.6% of that flora. Clearly, we have only begun to map the distribution of the flora in detail. In fact, we are still mapping the dominant species in the region.

Lake Tahoe vegetation and wildlife maps. The New Year's Flood of 1997 was a harbinger of a year filled with startling events in the eastern Sierra Nevada (Horton 1997). The world-famous transparent waters of Lake Tahoe had lost 8 m of clarity in the previous 32 years (C. Goldman *in* Elliot-Fisk et al. 1997), leading to a serious examination of the causes. In its final report to Congress, the Sierra Nevada Ecosystem Project cited loss of water clarity, drought, disease, and threat of catastrophic fire (Elliot-Fisk et al. 1997). President Clinton then convened a Presidential Summit at Lake Tahoe in July 1997, a result being the declaration of Lake Tahoe a national treasure. The President initiated a large cooperative effort between the federal government, California, and Nevada that would preserve the lake (Clinton 1997). The federal portion of the $900 million funding for 10 years of monitoring and restoration projects received final congressional

approval in November 2000 (Las Vegas Review-Journal 2000a).

To understand the ecosystems of Lake Tahoe, it is necessary to have a reliable vegetation map. Fortunately, by the time of the Lake Tahoe Presidential Summit, the GAP projects in both California (Davis et al. 1998) and Nevada (Edwards et al. 1996) were complete or nearly so. It seemed simple to splice the maps, which the GIS technicians at a laboratory at the University of Nevada did. The resultant hybrid map of the Carson Range had serious problems that led the Director to call me to see if I could devise a quick fix.

I began by collapsing the two different classification schemes used on the maps to a simpler set of fewer classes (14) that were held in common by both maps. However, in the best reclassification scheme that I could devise, only 40% of vegetation classes along the edges matched. Even at the structural level of forest, shrubland, and meadow, only 62% of the vegetation across the state boundary agreed. The only solution was to start over, and so I began developing new vegetation and wildlife maps for the Carson Range. I had one assistant and two months in the field to map 55 cover classes across 1340 square kilometers at 1:48,000 scale. Given so little time and so much ground to cover, the distributions I was concerned with were mainly the woody species. Nevertheless, this work yielded 7 new county records for 5 conifer species; this in a world-famous area within 100 miles of 2 major universities.

The maps I produced for the Carson Range covered only about half of entire Lake Tahoe basin, but their total cost was a mere $36,000, or 0.04% of the $900 million earmarked for Lake Tahoe restoration. Further, this database is versatile, serving multiple functions simultaneously due to how the data were structured. The complete set of cover classes can be converted easily to structural classes or to wildlife classes according to the wildlife habitat types of California (Mayer and Laudenslayer 1988). In the attribute table, each forest polygon has a species list, in descending order, of the arboreal species. Species with an attendant collection in the polygon are noted. Further, the design of the map and accompanying attribute table lend themselves to further augmentation with species-specific information in the future.

Nevada Science Teacher Enhancement Project (N-STEP). What better way to promote high school science education than to introduce teachers and their best students to the construction of a scientific vegetation map in a remote Nevada wilderness? I thought this was my idea, but I learned later that Jepson (1934, 1935, and 2001, this volume) was doing something similar at U.C. Berkeley 80 years ago. It was Jepson's student who made the vegetation map I admired the most (Wieslander 1940),

and this project collected more than 20,000 vouchers now at U.C. and elsewhere (Ertter 2001).

My teams' efforts in 2000 resulted in the discovery of a new Nevada record, *Disporum trachycarpum (David Charlet 2649 and Orne Grant UNLV, RENO).* A key to this find was that our group had a visible presence in and demonstrated respect for the local community. In fact, this find was in Jarbidge Canyon, merely 5 weeks after and 5 miles from the Jarbidge Shovel Brigade protest (San Jose Mercury-News 1999, Times-News 2000). The ironic twist is that we were led to the plant by a protester and resident who had lived there for decades.

GAP and re-GAP projects. GAP maps exist for all the states, and some states are beginning re-GAP projects (Scott and Jennings 1997). Regardless of the status of the GAP map of your state, GAP projects are opportunities to conduct species inventories while mapping vegetation. We should grab this opportunity and either improve the map during the re-GAP project, or ground-truth the existing GAP map. At the same time, we can conduct species inventories and collect vouchers, thereby improving the map, our herbaria, and our floristic database.

Where Is the Money?

Big money is spent on our wildlands in two relevant areas: fire and restoration following fire. For example, Nevada's first fire in the 2000 season, the Buck Springs Fire, conveniently occurred in the Spring Mountains in sight of my house as I was preparing this manuscript. I was shocked to learn that it cost $1 million to fight this 2000 acre fire (Las Vegas Review-Journal 2000b). One helicopter alone costs $53,000/day + $4000/hr. I admit it occurred to me that the daily fee is greater than my annual salary as a community college professor.

But that was just one little fire in an ongoing firestorm. In early July 1999, a Nevada official declared the fire season was "of Biblical proportions" (Reno Gazette-Journal 1999a) and the season ultimately consumed 1.8 million acres in Nevada (Los Angeles Times 1999). Fire-fighting costs for the 1999 fire season in Nevada included $6 million incurred by the state and $225 million by federal agencies (Reno Gazette-Journal 1999b). The crisis led Nevada Governor Guinn to announce what is probably the largest restoration project in the history of the world (Reno Gazette-Journal 1999c), with $15 million in restoration costs anticipated. So for the 1999 cost of fires in Nevada alone, there is a price tag of $246 million. Another 660,000 Nevada acres burned in 2000 (Western Great Basin Interagency Fire Center 2000) and restoration plans are proceeding (Las Vegas Sun 2000). Nationwide, the Secretaries of Interior and Agriculture recommended to the President in September 2000 that $2.8 billion be spent for wildland fire programs, including $150 million for post-fire stabilization and restoration (USDA Forest Service 2001).

Nevertheless, I must ask myself, what species will be seeded and what seed will be used? These questions lead me to an answer to another question: How can species-level inventories fit into this spending? The answer is the seeds. Due to high demand and low availability, sagebrush seed now sells for up to $100 per pound, up from $30 per pound in normal years (Las Vegas Sun 2000). Here is a way to help floristic surveys to pay for themselves during the short term: include seed collecting activities with voucher collecting and ground-truthing.

In addition to our ignorance of the flora and its precise distribution, there is much disagreement about what "restoration" is (Billings Gazette 2000; Elko Free Press 2000). This situation has led the western USA to what I have called elsewhere a "biogeographic crisis" (Charlet 1999). This crisis, as relevant here, involves species distribution, relative population levels, and the use of non-local or non-native seed in restoration projects.

Even in areas where we have a good idea of the flora's distribution, when large fire and flood emergencies occur, there can be no consideration for replanting the region with seed from local populations. We use what seed can be bought, no matter what the source. The introduction of other gene pools into a breeding population is background noise to the biogeographic signal present in the population's genetic diversity, and may compromise the population's long-term stability in the area. Further, these introductions threaten our ability to use our powerful new molecular biology techniques that allow us to look at a population's DNA and to examine the nuts and bolts of its evolution. Great Basin ecosystems are reacting to recent changes in fire frequency and timing (Tausch and Nowak 2000) as well as water diversions and development (Castelli et al. 2000). Biogeographic patterns are clouding, and these changes may be irreversible. It is essential that we use the correct seed in the correct places, and we cannot do this without baseline data and an established seed bank, both organized at the population level.

Conclusions

We can combine vegetation mapping with inventories by embedding polygons with species data into a GIS, and these species distributions should be documented, whenever practical, with vouchers. We also should collect seeds from the areas where we do our inventories and vegetation mapping. To be successful, the efforts of academia, agencies, and the public need to be coordinated and complementary.

Our knowledge deficiencies include ground-truthing and species inventory. To correct this, we must convince the public, legislators, and agencies that knowledge of this kind is inherently valuable. We need to take it upon ourselves to persuade ev-

eryone that this basic knowledge is valuable, and spending money to obtain basic knowledge is a good investment. Clearly, our restoration can only be as good as the information available. There is money: a mere 1% of $15 million restoration costs for the 1999 Nevada fire season could yield $150,000 for species inventories and vegetation maps. Nationwide, only 1% of the $150 million earmarked for restoration following the 2000 fire season could represent $1.5 million for a large national survey.

The health and management of our ecosystems has captured the attention of both the public and its elected representatives, especially since the 2000 fire season consumed 7.3 million acres in the USA (National Interagency Coordination Center 2000). These fires cost hundreds of millions of dollars to fight and hundreds of millions more in lost revenue. This public interest led the Western Governor's Association to have wildfires as the topic of their Winter 2000 meeting (Billings Gazette 2000). Throughout these meetings and plans, agencies must act as if ecosystem processes are understood and the distribution of all species is known, and the public expects that the right decisions are made. But these things are not known. We are only now learning where the dominant species are, much less all the species in the flora. It is in the public's interest that we obtain the basic information on the distribution of the flora, but it is up to us to convince the public that this is so. Vegetation maps, species data, and local, native seeds: all are needed for good resource management. With a little more effort than required for the vegetation map alone, we can include species inventories and seed collections and so enhance these projects.

Stimulating collaborations and powerful consensus can only arise when all parties are involved. We botanists, regardless of our affiliation or "amateur" status, need to cultivate relationships with every group. If we do, we will probably be surprised at what a tremendous pool of expertise and knowledge to which we have access. Local citizens are botanist's allies. They live on the land, have intimate knowledge of their landscapes, and can take us to their special places. Agency land managers and scientists are also botanist's allies: they got involved because they love the land and they love to serve the public. Outdoor recreationists are our allies too, as indicated by their choice to play outside on the land rather than in the gym. I would be remiss if I did not mention that more than once recreationists saved my crippled vehicle and me. Academicians are allies, especially if you come bearing good data and fine collections. Surely all parties will find common ground in the need to know what is on the ground and why, before we spend public money to restore it.

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ELECTRONIC ACTIVITIES OF THE UNIVERSITY AND JEPSON HERBARIA

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This review treats computer activities that are carried out as part of the institutional agenda of the University and Jepson Herbaria. Of course, individual workers in the Herbaria depend on a variety of programs daily: e-mail has replaced to some degree letters and telephone calls and has gradually claimed an increasing part of our time. Word processors and spreadsheets have nearly completely replaced typewriters. Programs that manipulate DNA sequences and generate hypothetical phylogenies are used by several of the staff and their students. Institutional use has as its nucleus the database developed by the Specimen Management System for California Herbaria (SMASCH), the continuation and maintenance of *The Jepson Manual,* the revival and furtherance of Jepson's Flora, publication of information dealing with nomenclature (including typification), and publication of information dealing with the history of the Herbaria.

The electronic activities can be grouped into three broad classes (which overlap considerably):

Curation—concerns of day-to-day operations of the Herbaria;

Publication/Education—information made available to colleagues and the general public

Interactive outreach—uses which allow the Herbaria to benefit from the knowledge of the general public, as well as outside botanists, both amateur and professional.

History

Computerization of the Herbaria began in 1982 when Thomas Duncan, a pioneer in computerized taxonomy, assumed directorship. Supported by a succession of grants from the National Science Foundation, computerization was fostered by the Specimen Management System for California Herbaria (SMASCH) which began in 1991. As SMASCH got underway, Duncan moved to found the University Museum Informatics Project, which was closely associated with the development of SMASCH. Although SMASCH was conceived as a confederation that would include many western herbaria, only the University (UC) and Jepson Herbaria (JEPS) were able to obtain sufficient funding to proceed. SMASCH developed protocols for organizing the tremendous variety of specimen information into databases and for automating herbarium administrative procedures. The project consisted of a coordinator (Thomas J. Rosatti), a software specialist (Mickey Ellinger), and a data-entry crew, some of whom remained for nearly the whole project and others of whom were transient.

The SMASCH software comprises a Sybase relational database that is accessed by data-entry routines incorporating the X-window graphical user interface. The original goal of SMASCH was to capture all label and annotation information for each vascular plant specimen from California in UC and JEPS, and to supplement this with a high-resolution image. It became apparent early on that these goals were too ambitious, and as a result, imaging was restricted to specimens of special importance, and recording complete annotation history was abandoned.

By the end of its final funding period in 1999, SMASCH had computerized more than 300,000 specimens—all of the California accessions and all of the North American holotypes (which were among the specimens imaged). During the project, emphasis was placed on optimizing efficiency of retrospective data entry and as a result, optimal procedures for data retrieval were deferred. At present, data can be accessed via X-window screens, via direct Structured Query Language (SQL) queries against the Sybase data tables, or via a web interface. The first two methods are not usable directly by the public at large, but the web interface is available to everyone: http://www.mip.berkeley.edu/www_apps/smasch/. This interface, which is not yet complete, now allows users to produce a list of all specimens that:

1. have a certain scientific or common name, or
2. occur in a selected county (or counties), or
3. were collected by a given collector, or
4. were collected on a given date or range of dates, or
5. contain designated "voucher" information, e.g., indication of flower color, chromosome count, habitat information.

The criteria can be combined so that it is possible, for instance, to request specimen data of all specimens of *Pinus sabiniana* Douglas collected by Jepson between 1895 and 1900 in Napa or Solano counties. The interface also allows queries by collecting event (each collecting event being a unique combination of collector, date, and location). Thus one could retrieve all collecting events by Jepson in Amador County, and from that one could obtain any or all of the specimens collected at a given location. Web queries are made not against the

main database, but against tables extracted from the main database and optimized for retrieval speed. Therefore, the extract that is available on the web may lag behind the main database and not immediately reflect updates.

It is also possible to retrieve lists of names grouped by county for which the Herbaria have vouchers. This feature was added recently at the request of people constructing county-level floras and is an example of how we hope to modify our web publications to serve the needs of the botanical community.

In addition, the raw data have been made available to the CalFlora Database http://www.calflora.org/, where they constitute most (more than eighty percent according to figures on the CalFlora "Information about Datasets" page) of the specimen data available at the site.

The future of SMASCH. The database that was established by the SMASCH project will be maintained by the staff of the Herbaria and will be expanded as time and funding permit. The following database tasks are now part of Herbaria routine: Modification of tables to reflect revisions of identification or nomenclature; data entry of newly accessioned California material or of returned loans; corrections of inconsistencies in the data. The original methods of data entry were designed to capture information from sheets in the Herbaria—retrospective data capture. In the future we will have the chance to computerize specimens that are not yet accessioned, and for this we have explored new methods of data entry. Most collectors now make labels for specimens that they eventually deposit in UC/JEPS from databases or other computer files. When we receive new acquisitions in lots of several hundred, it works well to convert these databases or files to an intermediate format from which selections can be bulk loaded into the database. This reduces data entry to associating the collector's number with a barcoded accession number. This is being done now with new accessions from Dean Taylor, Lowell Ahart, and Vernon Oswald, as well as with several lots of specimens in our "backlog." We anticipate being able to handle the more than 100,000 bryophyte specimens deposited by Daniel Norris and specimens deposited by James Shevock similarly. We are also experimenting with data input via web forms. We have made available a label-printing form that can store data sent to it so that if the specimens in question are ultimately received, the corresponding data can be retrieved and transferred to the main database. We also have a web form that will allow curators to enter information from any previously unrecorded type specimens that they encounter in the main collection. We are working to enrich the web query interface to the specimen database in order to allow a greater range of queries and to permit users to provide feedback automatically keyed to the specimen or name they

are dealing with. There may be users who are willing to help us rectify inconsistencies in the database, if we make the process convenient. For instance, a user might be able to add location information to a specimen by looking up another specimen collected by the same person on the same day.

Electronic products relating to The Jepson Manual. *The Jepson Manual* (Hickman 1993) is a widely used reference book that could be converted into an electronic product in numerous ways. Because the copyright is held by the University of California Press, however, use of the *Manual* other than in the form in which it was published has not been pursued. The electronic files from which camera-ready copy of the *Manual* was printed have been translated in part into Extensible Markup Language (XML), and from this version we have extracted the names of the taxa and a variety of associated data, including distribution. Distribution is indicated in the *Manual* by citing the bioregions in which a taxon occurs. Bioregions are hierarchical (Hickman 1993, pp. 37–48): e.g., the Great Central Valley (GV) comprises the Sacramento Valley (ScV) and the San Joaquin Valley (SnJV), and is itself part of the California Floristic Province (CaFP). We have made a web application (http://ucjeps.herb.berkeley.edu/jeps-list.html) that uses the base map of bioregions from the *Manual.* The distributions are displayed on the map by expanding the composite regions and coloring in each smallest unit. The distribution records are modified as new information becomes available, and since the maps are constructed on request, they reflect current understanding of ranges. Because of this dynamic generation of the maps, there are no static pages for outside sites to link to directly. Furthermore, the URL for the page of a given taxon incorporates a compressed representation of the distribution, so the URL changes when the distribution changes. To circumvent this problem we maintain a simplified, but slower, access procedure for external links, whereby an incoming request that includes just the taxon name can be associated with other information. The tremendous quantity of taxonomic information available on the web often makes easy what was previously difficult or impossible. Much of the value of the web arises from hypertext links, but links are not easy to maintain—URL's change, out-of-date URL's remain in caches of indexing sites, methods of generating dynamic pages change with software modification.

One of the challenges of website development is making pages flexible enough that they may be used in ways that the authors haven't anticipated—without causing security problems. It is important to make each page independent of the pages to which it is linked from the main site, because context may be lost when visitors come from an unintended page, or from an index cache. Therefore, we try to identify each page—whether it is dynam-

ically or statically generated—with a title that is meaningful in any context, and that has links back to the Herbaria home page.

The Jepson Interchange. We have for some time been considering the possibility of using web technology to simultaneously track changes in California floristics, make available expanded treatments of California plants (i.e., more extensive than those in *The Jepson Manual*), prepare for the second edition of *The Jepson Manual,* and communicate with amateur and professional botanists interested in the California flora (see http://ucjeps.berkeley.edu/far_west_initiative.html for an exposition by Barbara Ertter of a distributed information system for native and naturalized plants). This project is now underway, having been enabled by a grant from the William R. Hewlitt Revocable Trust. The new project, called the On-line Interchange for Advances in California Systematics, or the Jepson Interchange (http://ucjeps.berkeley.edu/jepson_flora_project.html), will provide a continuously updated authoritative list of California vascular plants, provide treatments for taxa not covered in *The Jepson Manual,* account for names not included in the list (synonyms, misidentifications), and most importantly, provide a convenient forum for all interested persons to assist in cataloging the California flora and understanding California plants. We now have web forms which can be used to report new records, call attention to publications pertinent to the flora, revise distributions, suggest hyperlinks, or contribute other information. The contents of the forms will be stored automatically in a database and e-mailed to an editor who will be the first stage of an authorization filter that may also include *Jepson Manual* editors and authors and other specialists. All submitted information will be available on the web, but only information authorized by the editorial committee will be incorporated into the list of taxa. As an adjunct to the Interchange, and in collaboration with the Digital Library Project of the University of California and Xerox PARC, we will make available scanned images from Jepson's "*A Flora of California,*" which contain a wealth of details on California plants.

OTHER WEB PUBLICATIONS

Index Nominum Algarum (INA). The INA (http://ucjeps.herb.berkeley.edu/rlmoe/) is a card file maintained by Paul Silva at the Herbarium of the University of California. It contains nearly 200,000 names of algae (in the broad sense). Associated with the INA is a separate card file containing bibliographic references pertaining to algal taxonomy—the Bibliographia Phycologia Universalis, or BPU. Cards that have been added since 1988 have been printed from a database, and the data are available on the web. As a preliminary step towards entering the remaining cards (pre-1988) in a database, and to provide archival protection, the cards

have been scanned as digital images. These digital images can be used in conjunction with indexes approximately like the physical cards can be used, but they are available from more than one site. We are making indexes to the images in two ways: via optical character recognition, and via forms that allow users to help by entering index entries directly.

Purpus site. Carl Albert Purpus was a plant collector in western North America with an unpaid curatorial appointment at Berkeley. Barbara Ertter and Tom Schweich have innovatively combined the wealth of archival material in the Herbaria with specimen information to present historical, floristic, and related data about the North American collections of Carl Albert Purpus in a globally accessible and informative manner for use by students, historians, botanists, and interested laypersons (http://ucjeps.berkeley.edu/Purpus/). We hope to have a variety of similar web publications in the future.

Indian Ocean Catalogue. The Indian Ocean Catalogue (Silva et al. 1996) is a compilation of all published records of species and infraspecific taxa of benthic marine algae from the Indian Ocean. Published by the University of California Publications in Botany in 1996, it was converted to a web version during the reviewing process (http://ucjeps.herb.berkeley.edu/rlmoe/tioc/ioctoc.html). The web version, which was generated by filtering some 75 files marked up for the troff typesetting program, allows a variety of searches, and is updatable by user input.

CONCLUSIONS

Because we are dedicated to increased computerization in the Herbaria, it is well to consider some of the assumptions and consequences of the process. The advantage of computerization is not that the traditional mission of the Herbaria can be accomplished more cheaply and more rapidly, although this is sometimes assumed. In fact, computerization probably makes routine tasks more time-consuming and cumbersome. The real advantage is that tasks can be accomplished that were previously impossible, with concomitant increase of the value of the specimens and specimen data to the Herbaria, to other institutions, and to the public. As a simple example, during the production of *The Jepson Manual* (Hickman 1993), it was not possible for contributors to check the vouchered distributions of species they were responsible for without borrowing all the specimens or visiting the Herbaria. When the second edition is assembled, it will be simple to provide all contributors with electronic reports of all the UC/JEPS specimens pertinent to their treatments, with distributionally noteworthy specimens flagged for their attention.

A specimen database is institutional. It, like the rest of the Herbaria, needs to function in perpetuity. Resources need to be allocated to it forever. It must transcend hardware, software, and personnel. A sig-

nificant cost of computerization is the requirement for vigilance—not with respect to privacy or security issues, though these are important—but with respect to changes in hardware, software, and personnel. All of the changes must be accommodated, and neither too rapidly, which would lead to constant turmoil, nor too slowly, which might cause intermittent large disruptions.

The Herbaria depend on the University for networking, database servers, and expertise. As our computer applications come to be used by outside users, those users will be similarly dependent. As Internet applications become more common, we likewise depend directly on outside institutions.

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WILLIS LINN JEPSON'S "MAPPING IN FOREST BOTANY"

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Abstract

A previously unpublished manuscript written by Willis Linn Jepson in 1938 describes the preparation and value of vegetation mapping as a field exercise in a forest botany course at the University of California at Berkeley. The resultant maps, of different sites in the Oakland–Berkeley hills, not only represent an invaluable baseline for charting vegetation changes since the early 20th century, but also provided the initial impetus for A. E. Wieslander's Vegetation Type Mapping Project of California.

Introduction

Richard Beidleman and Barbara Ertter

Throughout his professional lifetime, botanist Willis Linn Jepson was dutiful about maintaining field books, as he called them. These pocket-sized, leather-bound diaries were used primarily for the purpose of recording the plants, often with detailed descriptions, that he encountered in his innumerable field excursions, especially throughout the state of California. But he would often include tidbits about people he met, article and books that he read, and anecdotes about other scientists, both old and new. And because he was continually thinking them up, he would write down suggestions for student projects under a heading "Subjects for Students," because he was a firm believer in "hands-on" science teaching.

Jepson's projects weren't restricted to just plant collecting, classifying, and preserving. As a result of his own field encounters, his professional interests stretched far beyond such narrow activities to involve plant physiology, genetics, evolution, ecology, and phytogeography. Because he believed in studying nature, not just books, he actually took many individual students and even entire classes out in the field. His suggested projects often involved field pursuits such as determining the most common plants in the Berkeley area, measuring the surface position of leaves of native species out-of-doors, or recording when native plants developed their flowers and leaves.

Probably the most provocative field project idea that Jepson came up with, usually for students in his botany courses, was for small teams of students to pick a natural site in the Bay Area and map in acceptable detail all of the vegetation. Frederic Clements, in his *Research Methods in Ecology* (1905) and his textbook *Plant Physiology and Ecology* (1907), described the use of quadrats and transects, and he even described "Formation Maps," the latter involving "an outline map in which the various zones, consocies, communities, etc., are shown." But few researchers, and even fewer students, were involved in the early 20th century producing "Formation Maps" until Jepson actually set his teams of students to work on these projects just a few years after Clements published his ideas.

Jepson's students were becoming involved in more than mere plant listing. The mapping projects were definitely ecological in format and indirectly of greater significance and potential than even Jepson might have initially predicted. When retirement in 1937 provided Jepson with more time for reflection, he not only started going back over all of his field books and adding embellishments, but he also began writing about some of his research and teaching activities. Among these manuscripts was one that dealt with the vegetation mapping project. Because of its outstanding historic value at a time when vegetation mapping and classification is receiving much attention (e.g., Sawyer and Keeler-Wolf 1995), Jepson's manuscript is published here for the first time.

In a sense Jepson was correct in claiming that he was responsible for initiating, through senior pre-forestry student A. Everett Wieslander, forest mapping as a widespread U.S. Forest Service program (Ertter 2001; Wieslander 1935; Wieslander et al. 1932–1945). However, there are chronological problems with the article, which Jepson wrote some 25 years after the pertinent events. Jepson initially stated that Wieslander and his classmate Frank Herbert approached him in 1912 about teaching a course in forestry for students in the College of Agriculture. This seems unlikely inasmuch as Jepson was on leave in 1912–1913. But at the end of his article Jepson wrote that the preparation of forest vegetational mapping in "its final character flowed directly from the work of my botanical laboratory back in the year 1914." Wieslander had had to take his upper division botany course from Harvey Monroe Hall because Jepson was on leave in 1912–1913. But during the next academic year Wieslander and Herbert were seniors (Class of 1914), when they reportedly got the idea of doing a timber inventory at Muir Woods and were sent by Dean Hunt over to talk to Jepson, who had returned to teaching by this time. This is unquestionably the correct academic year for the discussion

between Jepson and the two pre-forestry students about mapping at Muir Woods, and it is relevant that Jepson was in the Muir Woods area three times during January and February of 1914 (as indicated by his field notes).

In an oral history, Wieslander (1985) reflected that when he and Herbert approached Jepson about getting academic credit for a forest inventory and management project in Muir Woods National Monument, Jepson "became hysterical and he started to sob and cry like a baby," apparently because the College of Agriculture was "trying to make a forestry professor of me, and I'm a botanist." Anyone familiar with Jepson would have difficulty visualizing him in a sobbing mode, although he did have a quick temper. It is true that some 20 years earlier Jepson had been irritated when it appeared that botany would be put under the College of Agriculture. But he had always been sympathetic with forestry, both from an academic and commercial standpoint, having spent much time with lumbermen in the field during preparation of his *Trees of California* (1909) and *Silva of California* (1910), both slanted towards forestry. Jepson was furthermore an instigator, adviser, and favored lecturer for the U.C. Forestry Club, which started in 1912 (Wieslander, incidentally, was president of the club in 1913). He was instrumental in having forestry established as an academic program at the university, with the Division of Forestry becoming an entity in 1914 (Casamajor 1965). Indeed, for some time from 1911, Jepson's academic rank was Associate Professor of Dendrology. He taught many a forestry student over the years and enjoyed running into and providing help for these men when they became professionals. One could appreciate that Jepson might indeed have been a bit disgusted with two young students who wanted to do an economic forestry management plan in a national monument, which showed some immature poor judgment (as Wieslander later appreciated). Jepson's recommendation that the two young men conduct an overall woody plant mapping project at Muir Woods, with his help but without an economic focus, made sense and paved the way toward more comprehensive forest mapping and management, which would later be spearheaded by none other than Wieslander.

MAPPING IN FOREST BOTANY

WILLIS LINN JEPSON

(from an unpublished 1938 manuscript in the Jepson Herbarium archives; minor editing by B. Ertter)

> We first survey the plot, then draw the model.
> —Shakespeare, *King Henry IV, Part 2*

Mapping as a forest botany course exercise. From a very early period in the history of the flowering plant work in the Department of Botany there was at intervals occasional assignment of field mapping as part of the work in Botany. The idea was original with me. Such assignments were made to students doing independent work who expressed a wish for a field exercise of this kind. As the years ran on and the value of the work became more and more apparent, mapping was introduced into the Forest Botany course as part of the regular requirement. While field work had always been a regular part of the course, this matter of mapping natural areas was something quite new and unfamiliar.

Because new and unfamiliar, many students mistrusted on the first day of a term their ability to do any such thing, although it was in fact quite simple though requiring pains and a large amount of field observation. The students worked in pairs, sometimes in threes. Two students were thus assigned to each of various natural areas in the Berkeley Hills, sometimes in the Oakland Hills, infrequently in Marin County. Such a natural area was a small drainage unit, a gulch, a canyon, a creek basin, or a ridge. The first duty was to make on a manila sheet, 36 × 48 inches or somewhat smaller or somewhat larger, a preliminary sketch map of the area, plotting its natural boundaries, creeks, and rivulets, contour lines being drawn in by the eye. All landmarks were indicated, such as large trees, prominent rock outcrops, or knolls. If the area were a canyon, the student moved around the summit of the bounding ridge checking the position of his landmarks and the flow of the contour lines which indicated slope or elevation.

A more elaborate method was used by students who desired to take special pains. In the laboratory a large sheet of white paper was fastened to the wall; on this was projected by a lantern, enlarged as required, a section from the topographic sheet of the United States Geological Survey showing the area selected. The student then drew in on the wall-sheet the lines of his map with a pencil and afterward finished it in ink. Or, yet again, the student could make a free-hand enlargement of his area from a topographic sheet.

Having made his preliminary map, the pairs of students were now ready for detailed field work, the object being to map the plant formations (grassland, chaparral, or woodland), and after that the associations within each formation (Fig. 1). The occurrence of notable individuals were often recorded on the map, as well as various special biological features. A report upon the area, a description and discussion of the formations, and an annotated systematic list of species was prepared by the student to accompany the map.

This assignment had great training value for the following reasons:

1. The student was required to make a complete list of the woody species of his area, and he was, thus, called upon to perform an intensified bit of work.

2. In order to make a list of the species, he had to
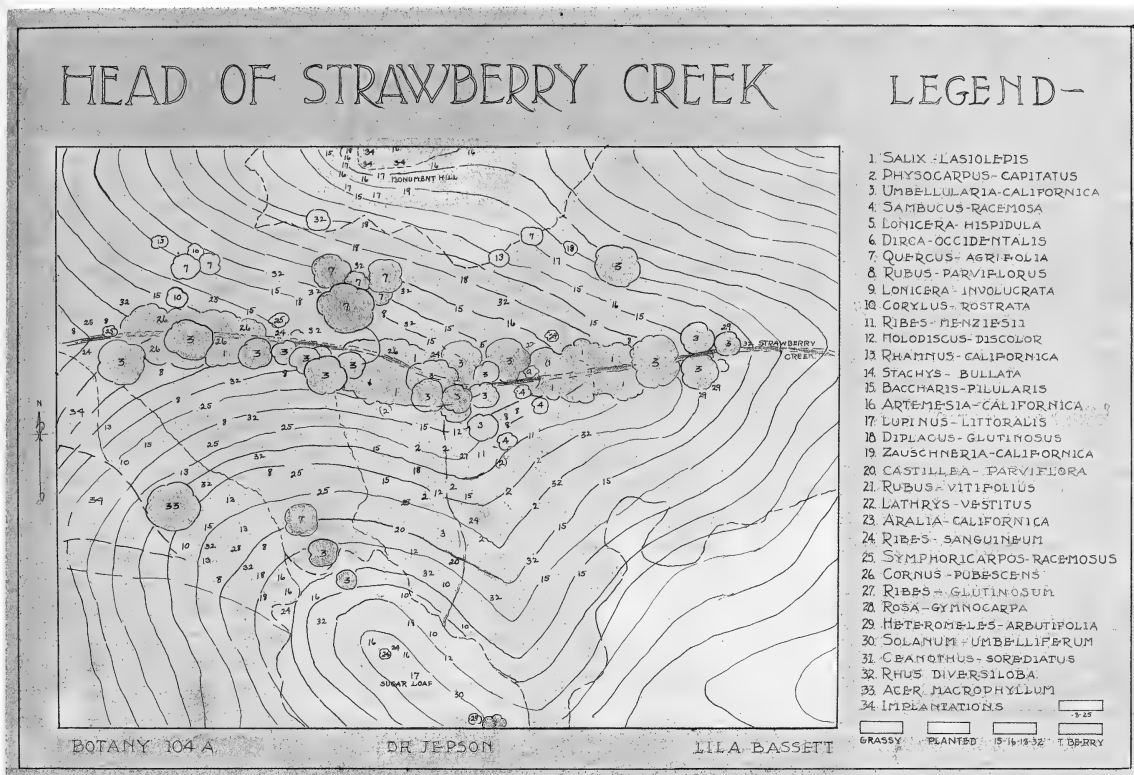
FIG. 1.   Example of map produced as a field mapping exercise in Jepson's Forest Botany course: *Head of Strawberry Creek,* by Lila Bassett, undated (original in Jepson Herbarium Archives). Although this particular example lacks a date, other maps in the collection were prepared 1918–1923. Strawberry Creek is in the Oakland–Berkeley hills due east of the main campus of the University of California at Berkeley. Although still largely undeveloped, large areas have been significantly altered by the introduction and spread of non-native vegetation, including various pines, *Eucalyptus,* and French broom (*Genista monspessulana*). Some of this vegetation is marked on Bassett's map as "Implantations" (34).

learn what a species is in the field. It was necessary to compare hundreds and hundreds of individuals of a given species and make sure that the differences amongst them were immaterial and that they truly belonged to one species. All species in the area had to be tested in this way. This was a highly practical exercise in the field recognition of species.

3. For his report, the student was shown how to observe various phenomena of the plant in order to determine as much as possible of its biology and life-history. He, therefore, became thoroughly imbued with the idea of the plant as a living thing, since no plant was ever quite alike from season to season, not even from week to week.

4. The student pairs being assigned to different canyons or ridges, there was thus cultivated a spirit of independence and self-reliance.

5. The area being given to only two students, they developed in it a sense of personal pride and possession. Even after the final examination at Christmas, it was sometimes noted that students continued to study their area. When asked why

they made yet another trip to it, the reply was: "We wished to see what it is doing now." So striking and significant, therefore, were the progressive changes in the life history to the close observer.

The sets of maps drawn by the Forest Botany students have been preserved (e.g., Fig. 1). They represent a valuable record of vegetation conditions in the hills at the time they were made. When handed in by a class just before Christmas, the entire set was posted on the laboratory walls and in the corridors of the Botany Building, where each year's exhibition created much interest amongst visiting botanists, zoologists, and agriculturalists. Dr. Joseph Grinnell [Director, Museum of Vertebrate Zoology] declared these plant survey maps had significance in relation to the localized distribution of mammals and birds in the hills.

Genesis of the Vegetation Type Mapping Project. In 1912 two students, F. B. Herbert and A. E. Wieslander, asked that I give a course in forestry for the benefit of the students in the College of Agriculture. There was at that time no division of forestry in

that college nor in the University. I refused to give such a course; the grounds of my refusal were that I was not a forester but a botanist in the College of Letters, and that my duties as a botanist more than consumed all my time and energies. But I added that I would give them work in botany which would be of the utmost value to them in all their lives as foresters and give them a real advantage over most foresters.

So I put them at the task of making a botanical map of the Muir Woods basin on the south slope of Mount Tamalpais. Since these two students belonged to the College of Agriculture, they wished to make an economic map of the area. I replied: "No. This must be a scientific map. To include only economic species would be ineffective because species of biological importance will be omitted; non-economic species tie in ecologically with economic species. The biological associations and interrelationships must be worked out; they are of fundamental importance. Moreover, a woody species thought useless today may tomorrow be highly valued economically. An economic map is partial and temporary; a scientific map is sound in concept and of permanent value." After a good deal of discussion, the two acceded to my view and went to work with great enthusiasm on their project. The final result was one of the most important reports on a natural area ever completed by students under the direction of my laboratory.

Nor did the significance of it end here. Both men won scientific positions in the United States Department of Agriculture, Herbert in the Division of Entomology, Wieslander in the Forest Service. In the course of time, the California Forest Experiment Station was established, and Wieslander was called to its staff. A highly important project was undertaken, that of a woody (vegetation) type map of all California, showing all the important associations in colors. The project was of the greatest scientific importance. Nothing on this scale had ever been done elsewhere in the New World, perhaps not even in the Old World.

The central governmental authority at Washington, contrary to Wieslander's recommendation, decreed after its fashion and custom that the map should be an economic map. Field work was pushed forward in southern California, and very soon, under Wieslander's effective driving methods, a considerable number of quadrangles were mapped and made ready for use. Economic use of the maps

by other branches of the Forest Service, especially by the various national forests, soon developed such that in certain particulars the maps were deficient though complete as to the original economic conception. The explanation was simple. New economic aspects developed so rapidly that it was proven repeatedly that an economic map was and must be from its nature transient and insufficient.

The federal authorities were finally prevailed upon after many years to reverse their decision, and Wieslander was authorized to carry out his original plan, that of a scientific map. Moreover, he was given a considerable appropriation to re-map the quadrangles in southern California. The map now became a scientific map, that is to say a botanical type map of the woody cover, and as such not was only of importance to foresters but to California botanists and to botanists everywhere. It appears to be, in reality, the most important and comprehensive botanical map of a large area ever undertaken anywhere on the earth's surface. It is naturally a satisfaction to consider that its final character flowed directly from the work of my botanical laboratory back in the year 1914.

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WILLIS LINN JEPSON—"THE BOTANY MAN"

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Near the tranquil summit of Cemetery Hill in the bustling valley community of Vacaville, California, stands a white Carrara marble headstone set upon a gray Sierran granite base. Carved on the tombstone is the name of Willis Linn Jepson, with the following inscription: "Profound Scholar, Inspiring Teacher, Indefatigable Botanical Explorer, born in Vaca Valley August 19, 1867; died in Berkeley Nov. 7, 1946. In the ordered beauty of nature he found enduring communion."

It was east of the Araquipa Hills, near Alamo Creek, where Willis Jepson's parents, William and Martha Ann, settled in 1857, coming out of Missouri in an adventure-fraught journey by bullock-drawn covered wagon, though earlier William had already experienced the gold rush days in California. At the Vacaville homestead, which later would be christened "Little Oak" for a seedling Valley Oak that sprang up in the woodpile, three daughters were born to the farming couple before Willis, and then a younger brother who later would die in a riding accident. About his boyhood Willis reflected that, "We had things. We had horses and cows and chickens. And flour from our wheat and fruits from the orchard. But we never had any money." However, as the family grew up it became a tradition to celebrate May Day with an outing. Throughout his lifetime, when his schedule permitted, Jepson would always try to continue the tradition, to be out in the field around May 1, "the best days in the year for the open."

Two things which Willis yearned for as a lad were a gun and books. Willis's father favored hard farm work and thought that reading was a terrible waste of time. The Jepson youngsters had one children's book of California pioneer stories, and Willis would sit by the pot-bellied stove reading the tales. He envied the neighbor boy who had copies of *Youth's Companion.* When he was able to save up a little money, the first thing Willis bought was a worn set of Charles Dicken's novels, which would remain part of his library, as did the tattered paperback about pioneers. This personal library burgeoned to the end of his life and eventually became part of the nucleus of today's Jepson Herbarium Library.

In those early days the Vaca Valley was sparsely populated beyond the village with farms and developing orchards, but much of the surrounding countryside was natural, with nearby unspoiled wooded canyons and chaparral-covered ridges, marshes and meadows, tree-lined creekbottoms. At an early age Willis, encouraged especially by his mother, developed an interest in natural history. As he later reflected, it was she who had provided him with an "almost inordinate love of dancing, of the songs of birds, of the sound of running water, of the flowing wind waves rippling the field of summer wheat—and all manner of joyous and pagan things."

But most formative, Jepson came to realize, was the opportunity as a teenager to attend the newly established Normal and Scientific School in Vacaville, which attracted able high school students from near and far. Under the tutelage of Wyandotte J. Stevens, A.M., the principal, young Jepson encountered chemistry, geology, zoology, astronomy, mathematics, Latin, literature, philosophy, and history. And then there was botany, which even included field trips and collecting. Here Willis was introduced to his first plant book, which may have been Volney Rattan's new *A Popular California Flora,* written especially "for beginners." One of his first preserved plant specimens was a *Lepidium nitidum* (Common Peppergrass) collected on March 6, 1884, probably around Vacaville. When his growing interest in botany occasioned a visit by the youthful Jepson to the California Academy of Natural Sciences in San Francisco, his reception as a budding naturalist by the venerable botanist Albert Kellogg and the younger Edward Lee Greene was something he would never forget.

At summer's end in 1885 Willis Jepson rode the train to Berkeley to take the entrance examinations for the freshman class at "the great U.C." Remarkably, he was the first young person from Vacaville who had ever applied to the university, and he found the initial experience so trying that he was "sick bodily and mentally" for days after the exam. Stress followed by relapse would unfortunately become, for Jepson, a familiar pattern throughout his lifetime. But there had been no reason for concern about the entrance exam, because he was readily accepted as a member of the Class of 1889, which four years later would graduate 42, including seven coeds.

In a sense, the four years at Berkeley provided a release from farming-town bondage. After a somewhat homesick freshman year, Willis came to life as one of the "Jolly Sophomore Boys." He became a leader in the Class of 1889 fights and yells, spending evenings and even afternoons at whist and

cassino and attending coeducational parties, plays, musicals, readings, and art exhibitions. It is historically significant that it was the Class of 1889 that initiated the university's first yell and set a precedent for future classes with: "Rah! Rah! Rah! Cal-i-for-ni-a! U! C! Berkeley! Zip! Boom! Ah!"

To be sure, the academic performance of Willis Jepson his first year had left something to be desired, with his poorest grades in geometry and algebra. But as a sophomore he proved somewhat more scholarly, at least outside of class, doing some botanical collecting for Edward Lee Greene, who had become Instructor in Botany in 1885, and among other pursuits Jepson initiated a recording of earthquake vibrations, noting that they generally occurred after eight in the evening. The high point of the second academic year, however, involved the wild sophomore celebration of Thanksgiving, which resulted in the kidnapping of several freshmen, running up and down Bancroft singing and shouting, and keeping "the town awake in diverse way[s], having three separate bonfires."

At the beginning of his junior year Jepson commenced an invaluable activity, namely keeping a diary. He prophetically promised himself to "record everything that is worth recording." "Not just a collection of dates—but rather a collection of thoughts." Although it started as what he called "a student's note-book," this activity within a decade would become a routine. Over his lifetime his entries, including innumerable plant collections and detailed descriptions, field trip experiences, anecdotes about fellow scientists, teaching and research suggestions, photography data, addresses, literature citations, would result in more than 50 compact, black morocco "Jepson Field Books," an invaluable record of a scientist's professional lifetime.

But the first diary, Jepson's "student's notebook," was concerned with his final two years at the University of California, when he became an extra-curricular achiever. He worked on the *Blue and Gold* year book, soliciting advertisements far and wide, and in his senior year he went on to become business manager, then energetic editor of the literary magazine *The Occident*. In his diary he demonstrated his literary and artistic talents by writing descriptively and repeatedly about the beauty of San Francisco Bay sunsets. On campus he enthusiastically attacked fraternities and the university administration. On the other hand, he attacked his course work with less enthusiasm, especially Political Economy and U.S. History and Constitutional Law. His grade in Zoology was a disappointing C, and at one time he was close to flunking chemistry and German. He worried constantly about examinations, and once, after getting only 14 hours of sleep during 48 hours of cramming, he was "utterly broken down."

The academic bright spots were his occasional botanical excursions with classmates, including Victor Chestnut, who would later become an important government scientist. But more influential was his continuing relationship with botany professor Greene. During a week-long illness ("sauer-bawled" in student parlance), Greene saw to his disciple's well-being, plying him with medicine and hot tea. And as Jepson reflected, "How many profs, I wonder, would walk a mile on a cold morning to build a fire for a sick student?"

Despite being ill the last two months of his senior year, Jepson still graduated with his favorite Class of 1889. Among interesting graduation statistics, Jepson at 160 pounds was 15 pounds heavier than the class average; at 5'10", he was 1½ inches taller than the class average, and after graduation he would eventually exceed 6 feet. His college occupation, as cited in the *Blue and Gold* year book, was "fire eater," his future occupation "Lobbyist," and his favorite beverage "Calves' Blood." Hmm. His most famous classmate was Lincoln Steffens, whose future occupation was forecast as "Would-be Aristocrate," but instead Lincoln became an astute muckraker. Decades later, Jepson, demonstrating his continued dedication to that memorable Class of 1889, would actually serve as its class secretary, soliciting news of his remaining alums.

Encouraged by Greene, Jepson now embarked on a graduate program, was appointed Assistant in Botany in 1891, and on April 20 commenced the field work at the Sutter Buttes that resulted in his first publication, "Botany of the Marysville Buttes" (*Torrey Botanical Club Bulletin* 18, 1891), in which he reported 110 species of plant. When Greene read Jepson's rough draft of the article, he told Jepson that the manuscript was too neat, that "The New York people would remark over its pedantic preciseness." So Jepson roughened it up a bit before submitting it.

That fall Jepson became president of the newly formed Chamisso Botanical Club on campus, whose initial purpose was to generate a list of plants growing within 20 miles of the foot of San Francisco's Market Street, and which held frequent meetings into 1897. In 1892 he joined a small, select group of individuals, headed by John Muir, to create the Sierra Club. The following year in early April Professor Greene and Jepson were in the field together, investigating the plants of the Marin Peninsula and northward. Jepson designed a spring garden of native plants at the University, and with Greene's help he started the botanical journal *Erythea*, which brought the young editor to the attention of a wide array of scientists. At Greene's botany laboratory and herbarium in South Hall Jepson was busily pursuing taxonomic work, with particular emphasis on Umbelliferae, Polygonaceae, and Chenopodiaceae, together with Marshall Howe, Joseph Burtt-Davy, and Ivar Tidestrom, all members of this botanical quartet destined for distinguished futures.

In 1894 Jepson first formulated plans for his magnum opus, *The Flora of California*. As early as

1887 he had begun numbering his plant specimens, but the early efforts proved inadequate. He finally formalized the numbering in 1899 and set aside numbers 13,334–15,095 for those earliest specimens. He always claimed that he was responsible for starting the university herbarium. Eventually he would almost frenetically build up his own personal herbarium, separated about 1905 from the university herbarium, by himself and through a growing cadre of collectors around the state, as almost exclusive reference material for his writing of the *Flora*. Surprisingly enough, Jepson would later emphatically aver that "The Herbarium will be my monument, more than the Flora." And today the Jepson Herbarium at the University of California does indeed constitute the "monument," associated with, but still distinct from the University Herbarium.

The mid-1890's became a period of ferment at the University. In 1895 Greene left Berkeley for Catholic University in Washington, D.C., taking with him not only his own herbarium but many of Jepson's specimens. University of California factions were divided between obtaining a new head for the department of botany or, as Dean of Agriculture Eugene Hilgard urged, putting botany back under agriculture.

Greene himself felt it better to let his "young team" handle the existing botany department without a chairman for a year. In February Jepson was granted a leave of absence with salary to study at Cornell University and was away from Berkeley until July. Meanwhile he somewhat shocked Greene by reporting that he had entered his name for the chairmanship; but as backup Jepson had also made an application to Oregon State College (Corvallis) "to fill the professorship of botany" at that institution.

On August 12 the *San Francisco Examiner* carried a blurb about Greene's leaving and went on to report that "Willis Linn Jepson, who was Professor E. L. Greene's assistant in the botanical department, will succeed his old chief." There were others, including Professor Willard Rowlee of Cornell University, who anticipated that Jepson would indeed become chairman of botany. Greene, however, pointedly reminded Jepson that all he had promised was to request an instructorship for Jepson, not any chairmanship.

By late summer, although a separate botany department had been retained by the university, the new chairman and full professor was a Dr. William Setchell, who had earned an undergraduate degree from Yale and a Ph.D. from Harvard. Actually, Hilgard had hoped to entice the distinguished Charles Bessey from the University of Nebraska for the position, but California's offer had fallen short. Two decades earlier, when Bessey had taught a three-week-long course on economic botany at the new university in Berkeley, he had been perfectly happy with a stipend of $300.

Dr. Setchell was slightly older than Jepson, was from the eastern Ivy League establishment, with a well-to-do New Haven family background, sported a Phi Beta Kappa key, already had his Ph.D., had been assistant professor at Yale, and was a "bombastic" extrovert. The more introspective Jepson received an appointment only as an instructor in botany from the Regents on August 13, 1895, with a salary of $1,200. Congratulations for this appointment shortly arrived from his former classmate Victor Chestnut, who was familiar with Setchell and optimistically commented that "He will speed up the biological side & will need you badly to bolster up the Systematic side. Hold your fort." But the western farm boy from Vacaville, although with an egotism of his own, undoubtedly felt outclassed by Setchell; and in academia Jepson, at least in his own mind, would increasingly "suffer" beneath that domineering shadow until Setchell's retirement in 1934. However, Jepson too would later sport a Phi Beta Kappa key, just like Setchell.

In the fall of 1896 Willis Jepson received another semester's leave of absence with salary, this time to work up his California collections at Harvard's Gray Herbarium under curator Benjamin Robinson's direction. At the beginning of his trip, he received a solicitous letter from his new department chairman to take care of his health and be sure to look up the Setchell family when he passed through New Haven, Connecticut. When Jepson's productive stint at Harvard came to an end, he did visit New Haven, saw the Setchells, and enjoyed a dinner with the famous William Brewer of Yale's Sheffield Scientific School. Although Brewer's plant collections from his "up and down" days with the early California Geological Survey would not even come close to what Jepson would collect in his own lifetime, the number of California miles which Brewer covered in the California wilderness during the Civil War years may well have exceeded Jepson's eventual three-score years of extensive tramping.

By this time Jepson had already been on his own exploratory California treks. His first of many junkets to Yosemite National Park was in August of 1890, then two years later he was in the Yuba River Sierra, and in Mount Shasta in 1894. During July of 1896 he, alias "Dusty Roads," and Setchell, alias "Weary Wilie," had a companionable botanical excursion by horse and wagon to the Santa Cruz Mountains and then east across the San Joaquin Valley to Yosemite. The summer of 1897 found Jepson in the wild Yolla Bolly and redwood country of northwestern California, with former Cal football left tackle Loren Hunt as his able assistant, collecting new plants and recording the trip with his camera. Also, this was the first year that Jepson ever gave a public lecture, before a small audience isolated in the Santa Cruz Mountains. He talked, somewhat timidly, about the colorful massing of flowers in the springtime, illustrated with some of

the finest herbarium sheets he could find. He was well received, invited to stay overnight; and thus commenced a lifetime of popular lecturing. Indeed, 40 years later he would even be delivering a 30-minute radio broadcast from KLX, Oakland, on "The Message of John Muir" to celebrate that great naturalist's birthday.

On May 11, 1898 Willis Linn Jepson took the final examination for his degree of Doctor of Philosophy, with a major in systematic botany, minors in plant physiology and paleophytology. His thesis was on the flora of Western Middle California, and comprising his Sub-Committee were Setchell and Dr. John A. Merriam, paleobotanist and future president of the Carnegie Institution. More than mere years now separated the Jepson of the Ph.D. exam from the Jepson of the freshman entrance exam, as he answered such questions as "Development of taxonomic knowledge of the California flora," the "De Candollean System as modified by Bentham and Hooker," "California Plant Areas and Communities," "Periodicity of growth" in plants, and "Floral changes during the Mesozoic Period." His Ph.D. degree would be only the 10th granted by the University of California and its first in botany! It might well have seemed demeaning for Jepson to complete his degree under Professor Setchell. But that notwithstanding, "The Botany Man" was at the gateway of his professional career. And there was no better way to launch it than with a series of 6 lectures on botany, illustrated with lantern slides, sponsored by the University of California and presented on Friday evenings in March and April of 1899 at the California Academy of Sciences.

There would shortly be more than a purely academic experience ahead. A tradition was developing in the department of botany to have staff members spend summers out in the field. And 1899 was especially appropriate because it was the summer during which the Harriman Expedition, with its shipload of eminent scientists, was sailing into Alaskan waters. Thus it was that an intrepid quartet of U.C. young men including Setchell, Jepson, Hunt (now instructor with the U.C. Civil Engineering Department), and the new assistant in the botany department, Anstruther Lawson (later to become botany professor at the University of Sydney in Australia), set out from San Francisco aboard the *Bertha* on their own Alaskan adventure. The group photographs of the quartet on shipboard show Jepson reading Kipling while the other three were consorting with some of the female passengers.

Once in Unalaska, the U.C. group moved into the bishop's old home in the Aleut village of Iliuliuk next door to the cathedral and Indian boys' school. Non-smoker and non-swearer Willis was initiated into matesmanship by his devilish compatriots with a baptism of cigar and pipe smoke and volleys of vulgarities. But out in the field it was time for botanizing, with the four busying themselves collecting mountain higher plants and coastline lower plants, not to mention teaching the local Native American boys the fight yells of the University of California, and socializing with Harriman's scientists, including John Muir and John Burroughs, when the latter were briefly at Dutch Harbor. At summer's end the quartet was back in Berkeley. Setchell delivered his lantern-slide lecture, "A Botanical Trip to Alaska," for a university audience, while Jepson received from the university his appointment as assistant professor of botany. So would a new century be ushered in.

Assistant Professor Jepson was beginning a professing career which would extend until his retirement at summer's end in 1937, becoming an associate professor in 1911, a full professor in 1918. He embarked on an annual schedule that involved teaching much of the academic year, with summers and any other free time preferably out in the field. He developed strong ideas about botanical field work, asserting that it was not for weaklings. In the earliest days he traveled on foot, on horseback or with mule, and for longer trips by railroad where possible and otherwise with his camp wagon. When automobiles became the public's mode of traveling, he warned that "You must still go afoot if a real botanist. No field botanist should become soft and travel only in an auto."

He would sleep under the stars, using a tent only to dry his plants in, cook his meals over a fire, trespass and collect where he wished, even in national parks, and with nary a reprimand, bring along three presses ($16'' \times 11''$, of oak frame for lightness and strength, with straps of harness leather and nickel buckles and a leather handle), one of them for collecting and two for drying, a vasculum and a pick which he had designed himself, his knife attached by a buckskin string; and always mark in the field each collection folder with locality and specimen number. Eventually he prepared a collector's manual, which unfortunately he never published, commencing thus: "Exploring for plants in California. A handbook for making records, preparing specimens and guiding beginners in the ways of camp and trail."

It was fitting to start off 1900 with a new organization at the University of California, the Field Club, intitiated on January 20 and devoted to "prompting tramping trips into the region about the Bay," with Jepson being elected President. The summer of 1900 found Jepson and some colleagues far from just tramping around the bay, as they hiked into the southern Sierra towards the tallest mountain of them all, Mt. Whitney, accompanied by two dutiful mules, Hot Haste and Sierra, and a copy of Volume 1 of the *Botany of California* by Brewer and Watson, hardly a field-guide sized volume. It proved a small world in the high mountains, because who should be encountered but the University of California's Joseph LeConte, long-time professor of natural history and author of *A Journal of*

Ramblings through the High Sierra, which recounted his ramblings with the new 1870's University Excursion Party. Just a year later LeConte would pass away during a Sierra Club hike in Yosemite.

Although the *Flora of California* was Jepson's perpetual goal, ''a symbol of my life,'' he began pursuing a variety of other involvements. His Ph.D. thesis, *A Flora of Western Middle California,* was published in 1901, and the next year he completed a small *School Flora for the Pacific Coast.* With a growing interest in forestry, that was the summer he spent in the lumber country of northwest California, especially investigating the mall oak industry but falling in love with the redwoods.

When, in 1903, an influential group of Los Angeles citizens, concerned about forests and watershed protection, approached the University of California, President Benjamin Wheeler called upon Jepson and Professor Arnold Stubenrauch of the agriculture department(?) to conduct what turned out to be a very successful forestry summer camp at Idyllwild in the San Jacinto Mountains. The 10 lectures which Jepson delivered dealt with ''Life-history of a Tree,'' ''Classification of Forest Trees,'' and ''Forests of California.''

Pursuing this forestry interest, then, Jepson on his own began gathering pertinent information out in the field, becoming acquainted with lumbermen, and taking photographs related to the lumber industry in California, which culminated with the publication in 1909 of his singular *The Trees of California,* and next year the definitive *Silva of California*. He also incorporated more material on forestry in his botany courses, was instrumental in encouragement for a forestry school at the university, and when some of the students organized the Forestry Club in 1912, he, then as associate professor of dendrology, became a popular advisor and lecturer for the group.

Meanwhile, the first two fascicles of his *Flora* appeared in 1909, including gymnosperms, the willow family, oaks, and several other small families. The publications were illustrated with a few fine photographs by Jepson, and some line drawings, the three initialed by an inconspicuous M.H.S. being drawn by Mary H. Smith. Incidentally, only rarely, as they were to note, did any of Jepson's many artists over the years receive much, if any, recognition. The next fascicle, copyrighted in 1912, would include a lengthy section on Gramineae by U.S. Department of Agriculture grass authority A. S. Hitchcock. In future fascicles there would not only be detailed descriptions but extensive locality data for each species based upon herbarium voucher specimens.

The academic year of 1905–1906 was Jepson's first sabbatical leave as a professor, and in early July he was off for Europe as one of four American delegates to the Second International Congress for Agricultural Education, which met on July 28–29, 1905, at Liège, Belgium. Taking full advantage of his sabbatical, he then spent the fall and early winter in Great Britain, researching and recreating, with extended time at Kew Gardens where he actually encountered historic plant collections from California, including type specimens gathered by von Chamisso in 1816.

Then in early February he returned to the European mainland, making the continental tour from Paris to Italy to Switzerland, and finally to Germany, where he settled down in Berlin, hired a German conversation teacher, and interacted with eminent German taxonomists, especially at the Botanic Garden. In mid-May he was back at his favorite, Kew Gardens, and finally home to Vacaville in early August by way of Yellowstone National Park and the Columbia River. On every occasion abroad he was received as a distinguished visitor, dined and wined and regaled. Small wonder that in 1906 he was included among the 100 leading botanists in the United States in a report by Jaques McKeen Cattell.

During the summer of 1909 Jepson, for the first time, joined an extended Sierra Club summer excursion, this time in Yosemite and Hetch Hetchy. Jepson was in his element, hiking, collecting plants, taking photographs, giving a lecture on Sierra conifers and providing the farewell invocation. And since one of his hiking companions was John Muir, there was many a conversation between these two, which were recorded in Jepson's field book, including conversations about the proposed flooding of Hetch Hetchy Valley. Continuing for a number of summers Jepson would accompany Sierra Club trips, collecting, lecturing, reciting poetry along the trail, getting acquainted with a variety of outdoor-loving people from around the world, the groups sometimes including more than 200 individuals, covering many miles of the Sierra Nevada, and often taking up most of a summer.

Before Jepson knew it, another sabbatical leave year arrived, 1912–1913. Initially he had grandiose plans which included not only Kew Gardens and mainland Europe again, but followed by an around-the-world collecting tour. However, with his mother's health in question, he settled initially for his first retreat to the Mohave Desert, at the Waterman Ranch near Barstow with the late Governor Waterman's daughter Abby as his hostess. Abby had graduated from Berkeley in the Class of 1904, a president of Prytanean, the Women's Honor Society, during her senior year. Berkeley had been her home, but eventually she had to move to her father's desert ranch because of her health.

During this early June of 1912 at the Waterman Ranch, Jepson, alone and with Abby, botanized in the area, sometimes on foot, by horseback, or in Abby's rig drawn by ''the Blacks.'' This became a Mohave Desert field tradition which would repeat itself many a time. In years to follow, when Jepson's Mohave-bound Santa Fe train, and later his automobile, would drop down from the Tehachapi

Summit, reach the first of the Joshua Trees and swing into the open desert of Creosote Bush, White Bursage, and distant vistas, the university professor was able to cast off his academic robes, so to speak. As he once wrote in his field book: ". . . it caused my spirits to rise and at once I felt better in body as well as cheered and sustained in mind."

This first visit to the Waterman Ranch was for only 7 days, and then it was back to Berkeley. However, by the end of June 1912, Jepson was once more in southern California, this time to join the Sierra Club's 5 week excursion through the mountainous Upper Kern River Sierran countryside. Again Jepson was in his element, hiking through wilderness with 200 club members and 40 assorted attendants, botanizing, lecturing, and in mid-July garnering alpine flowers on Army Pass at 12,000 feet, just south of Mt. Whitney. This hegira finally terminated on the east side of the Sierra at Lone Pine the end of July.

The best was yet to come, during the autumn of his sabbatical. In mid-October Jepson was once more in the Mohave Desert, first at his tent site on the Waterman Ranch, and then joining his Sierra Club hiking companion James Rennie at Needles. There the two men bought a rowboat for $15, named it *The Lotus,* and proceeded down the untamed Colorado River to Yuma on a 15-day collecting adventure, a journey along the edge of the new state of Arizona replete with white water, a sunken boat, a presidential election, and Giant Saguaro photo ops.

The remainder of Jepson's leave was spent close to home, but filled with excitement. Since 1902 he had been dreaming about a botanical society for California. So on April 12, 1913, at his call some 20 people gathered in the meeting room of the Oakland Public Museum to discuss the creation of such a society. Two weeks later at a general organizational meeting in Oakland the California Botanical Society was established, and Dr. Jepson not only was elected its first president but would serve as editor of its publication *Madroño* for many years, and before summer's end would make arrangements for its first annual banquet speaker.

During late spring of 1913 Willis Jepson was headed once more for the Mohave. Abby Waterman picked him up at the train station with her road team, and he stayed again in his tent above the ranch. Soon out into the desert, at Calico Wash, he paused to write in his field book: "Sitting here on the ground studying flower parts under the lens is a pleasant occupation. When one's eyes tire there are the desert ranges stretching one beyond another, and a soft breeze blowing from the west." Eventually he traveled on to the New York Mountains, Needles, and finally to San Bernardino where he went on a brief collecting trip with his friend Samuel Parish, the premier amateur botanist in southern California, before returning to Berkeley.

It was now time to think seriously about a Cal-

ifornia Botanical Society banquet speaker, and Jepson had candidates. The International Phytogeographical Excursion, with its entourage of important European and American botanists, had been touring the Middle West and southern Rockies during the summer of 1913, and in September was coming to California as the state's first organized botanical excursion. Here Jepson would guide the group through Yosemite National Park. After a week enjoying the incomparable Yosemite under Jepson's leadership, the excursion traveled by train to Oakland, visited Luther Burbank at Santa Rosa, then proceeded to Muir Woods with Jepson, where Alice Eastwood of the California Academy of Sciences joined the assembly. Finally, the congregation went down to the Monterey Peninsula, where the botanists were the guests at the Carnegie Desert Laboratory's Coastal Laboratory in Carmel.

When the train arrived in Oakland from Yosemite on September 12, there awaited an evening's entertainment. It was the inaugural banquet of the California Botanical Society, with eminent and undoubtedly exhausted phytogeography speakers fortuitously arranged by Jepson: Professor C. von Tubeuf from the University of Munich and Dr. Adolf Engler, Professor of Botany and Director of the Royal Botanical Gardens at Berlin, where Jepson had sojourned in 1906.

Jepson's teaching assignments during the academic year of 1913–1914, including a routine Botany 1 course, must have seemed a letdown after all the events that had transpired the previous 2 years. But he was back to the Mohave by late April and throughout May. This time Jepson, accompanied by Abby Waterman, her sister Dr. Helen Waterman from Berkeley, Mrs. Rice, and Herbert Manson (the Waterman Ranch foreman) embarked upon a month-long desert circuit from Barstow to the Old Dad Mountains, Ord Mountains, Twenty-Nine Palms, Indio, Palm Springs, San Bernardino, and back to Barstow. Then in August Jepson made a collecting trip up the Sacramento River to Dunsmuir.

With the arrival of fall Jepson's most disastrous academic year commenced, which rightly or wrongly would forever imprint its apparent consequences upon Professor Jepson's mind. In 1914 William Setchell suddenly announced that he would be taking a sabbatical leave starting in the autumn, and, as Jepson expressed it, "thrust the Department load almost wholly on me." There had already been increasing antagonism between Jepson and Setchell in recent years. Jepson was heavily preoccupied with his work on the *Flora,* continuing to build up his herbarium by collecting trips, preferably long ones, in every available moment; had what seemed to him like a demanding teaching load; and had never cared for administrative duties though he might secretly have wanted to be department chairman.

Despite the ensuing travail, Jepson did manage

to survive the academic-year demands while Setchell was absent, and was actually able to spend productive time in the field from late May until late July of 1915, especially doing field work in the central Sierra around Columbia and the middle fork of the Stanislaus River. By mid-September of 1915, however, he "snapped," and went into the sanitarium at St. Helena, near the home of his sister Mary Elizabeth and her husband Frank Pellet. This sanitarium would become a frequent retreat for Jepson because of its "tranquility." "One finds there an atmosphere of peace, quiet, good cheer and hopefulness." When Jepson requested another leave of absence from the university to recover from his breakdown, the dean reminded him that he had just had a leave with pay 2 years earlier, so this requested leave would have to be without salary.

By mid-December of 1915 Jepson left the sanitarium to continue his convalescence in Barstow at, naturally, the Waterman Ranch, where he remained until the end of March. The Waterman Ranch, obviously, had become Jepson's favored retreat when he sought prolonged respite. And for those who have wondered, this explains the dedication which Jepson in 1936 so poetically penned for the second volume of his *Flora*: "Abby Louise Waterman. Daughter of the desert and of a race of sages, penetrating observer of the arid wastes of mesa and playa, protector of the desert men against the errant flow of circumstance, to her is inscribed this dedication page of the second volume of the Flora of California by the botanical traveler, who, driven from pitiless ranges and stone-dry hidden valleys in the year nineteen hundred and fifteen, found elemental shelter at Waterman Ranch in the heart of the Mohave."

Much of the Barstow stay, this time, was not productive for botanizing, but during the winter months Jepson kept busy observing birds, preparing what was probably Barstow's first winter bird inventory. By April Jepson had recovered sufficiently so that he could make a trip to the San Diego Exposition, which he felt was a disappointment, "unless for persons who seek merely to be amused." Then he carried out some field work in southern California before returning to Barstow, then Berkeley and Vacaville.

Although Jepson would always look back on that Setchell sabbatical period as one of the two major calamities in his professional career, the other to come in the mid-1930's, he did actively return to his teaching and field research routine by 1917, spending May of that year in Death Valley and from mid-July into early August in the White Mountains, busy collecting more plants. His interest, however, began to focus on coastal redwoods, with which he had become enamored during earlier field trips in the northwestern California redwood country. There was growing statewide interest in redwoods, including a drive for a redwood state park; in July of 1919 the Save-the-Redwoods League was established, with Willis Jepson as a member of its Executive Committee. Immediately Willis Jepson embarked on more than a decade of public lectures around the state in support of the League and preservation of redwood stands.

During the early 1920's Jepson was at work on a new book, which would be published in 1923–1925 as *A Manual of the Flowering Plants of California* a 1200-page tome in a single volume (unlike Leroy Abram's four-volume *Illustrated Flora,* which began appearing at the same time, published by the Stanford University Press). Although the book was put out by the Associated Students Store at the University of California, the entire cost was borne by Jepson; and through the years he would frequently complain that while other faculty works were published at University expense, his never were. The *Manual* was not intended to replace Jepson's projected *Flora,* but with its comprehensive keys, many line drawings, and detailed species descriptions, the *Manual* would be the sole California botanical bible until the publication of *A California Flora* by Philip Munz and David Keck in 1959.

It was in September of 1925 that Jepson finally moved into a home of his desire, at 11 Mosswood, a several-storied Mediterranean style mansion with red tile roof, on a prominence looking down into the lower end of Strawberry Canyon and the university stadium, well beyond the academic campus. Largely designed by Berkeley's famous architect Julia Morgan and beautifully landscaped, with several attractive gateways into its walled enclosure, the home was embellished by Jepson inside and out with ornamentation both floral and faunal. In the downsloping first floor, paneled in redwood, was the fine large library and herbarium drawers. The key to the cabinet which held his type specimens was labeled "Holy of Holies."

Above, on the main floor, was the front room, with comfortable chairs and scattered Persian rugs, and three large overflow bookcases. The great west window looked out across San Francisco Bay from San Mateo north past Tamalpais to San Pablo Bay, a vista which Jepson especially enjoyed in early evening, with the twinkling lights of the metropolis. Among the many pictures on the wall was a large beautiful oil painting of the Suisun Marshes, with the mountains beyond and "magnificent clouds at which I look a great deal!" Above the brick fireplace in the living room was a redwood panel with an engraving of a California Quail on one side, and on the other side Jepson's boyhood favorite, the Acorn Woodpecker (which he incorrectly called a "California Red-headed Woodpecker"), and in the center an engraving of "Golden Eggs," a yellow Oenothera (*Oenothera ovata*) that used to carpet the campus when Jepson was a student. On either side of the entryway into the dining room were additional recessed bookshelves. Even in the sparse bedroom, with its spartan wood-frame bed there was a bookstand by the bedside. Engraved into

wood paneling on doors were images of plants and birds, while at the front entrance, which faced the upper hillside, there were in the framing of the tall entrance door California Quail amidst twining runners of oak.

It was rumored among the graduate students at the time that Jepson had prepared the home for a prospective wife, but alas she apparently married someone else. There is no question that Willis Jepson, over a span of many, many decades, was both a romantic figure and eligible bachelor in the imagination of many women of his acquaintance, whether he had met them as one of his students on campus, on a Sierra Club trek, at a scientific meeting back east, or even in London during a sabbatical. He was tall and lean, with craggy features, "rugged, like a tree" as one of his former women students reminisced. His personal correspondence abounds with appealing notes. But, of course, Jepson would remained forever a bachelor.

In December of 1925 Professor Jepson was off on a major sabbatical trip, this time to the Middle East with William Bade, dean at the Pacific School of Religion in Berkeley and a biblical scholar. This would turn into an extensive journey encompassing essentially all of the countries surrounding the eastern portion of the Mediterranean Sea, with special emphasis on Egypt and Palestine. Jepson toured famous landmarks from the pyramids and Karnak, to Mary's Well in Nazareth and the Dead Sea, collected plants in the desert and among the cedars of Lebanon, visited institutes and universities, met Muslim botanists, Arab shepherds, camel drivers, bedouins, biblical scholars, British soldiers, geologists, and archaeologists, and took enough photographs to prepare a hand-tinted lantern slide program upon his return to Berkeley.

In early June of 1926 Jepson went on to England from the Middle East, working again at his favorite Kew Gardens Herbarium until mid-July, as usual focusing on early West Coast plant collections. Then he scheduled a memorable trip to the Liverpool area on the trail of one of America's greatest frontier naturalists, Thomas Nuttall, the first botanist to cross from the Atlantic to the Pacific in 1834 and who, on his way back east in 1836, collected along the California coast from Monterey south to San Diego. Because of provisions of an uncle's will, Nuttall had to return to his native England in 1841, occupying Nutgrove estate near Liverpool until his death in 1859. Jepson was ecstatic at actually encountering Nuttall's grand nephew, Dixon Nuttall, who as a young lad had met Nuttall; and then locating Nuttall's old Nutgrove Hall (in 1926 it housed a girl's school) and his grave at nearby Christ Church. In 1934 Jepson would publish an article in *Madroño* about Nuttall's botanical excursion across America, the botanist heralded by the Missouri Botanical Garden as "The Father of Western Botany"; and on October 25, 1935, he would deliver a dedication talk at Spring Valley Lake for a Nuttall memorial there.

Leaving England in early August of 1926 on the *Orca,* Jepson stopped over in Ithaca, New York, to attend the Fourth International Botanical Congress at Cornell University. He observed that "One meets a bewildering lot of men here," many of them, of course, old acquaintances, the "most terrible bore of the Congress" being P. A. Rydberg of the New York Botanical Garden, who always seemed to dwell on trivial points.

During the 1920s the University of California botany department would move into the remodeled Palmer House and expand both its faculty, its roster of graduate and undergraduate students, and its laboratory courses. Jepson had developed the basic teaching philosophy that "every educated person should know, at least broadly, the native forests, shrubs and flowering plants in his own state, so that elsewhere he may be an intelligent traveler." He further felt that "the object of botanical investigation was to learn as much as possible about the plant and that every phase of the life-history possible should be represented in the record either by specimens or field notes. . . . Intelligent and critical observations with real things in view should be the student's aim, should be the things held in mind, not, as I say, merely to collect, but to study plants." In his actual teaching, Jepson followed the pedagogical pattern of Louis Agassiz. Especially with his graduate students, he would give adequate preliminary instructions, then pay no further attention until the student was ready to raise questions. Professor Jepson was always thinking up and writing down questions for students to contemplate, projects for them to pursue. One invaluable field exercise initiated by Jepson for botany seniors was to have them do a detailed vegetational map of some local site, an experience that in part provided the model for development of our modern vegetational mapping programs.

By now, Jepson had taught long enough to have generated a lengthy roster of former students, and often he would coincidentally run into one of them in the field, or hear from them by letter, sometimes with a query but often with a note of appreciation for a remembered course. He not only taught in the classroom but had the audacity on occasion to take his students, from beginning classes to graduate seminars, out into the field, even across San Francisco Bay by ferry to the Marin Peninsula. And during a pause in a field trip, he would often bring forth a favorite book, which he always had wrapped protectively in paper or from a book bag, and read aloud to the students, the likes of "The Ode to True Romance" or "The Old Three Decker" ("Full thirty feet she towered, from waterline to rail . . ."), Kipling and Stevenson ranking high among his choices. There were some students who appreciated such an exposure to the liberal arts, while others must have felt a bit embarrassed.

Among the botany faculty there were increasing schisms. Professor Setchell, as someone once noted, "liked to draw people around him." He was at ease with students, liked to be known as "Papa Setchell" or the "Old Boy" and in turn called his favorites "nieces and nephews." Jepson, on the other hand, "needed serenity and quiet in which to work." He received no informal nicknames from students, at least to his face, though behind his back Thomas Howell called him "Jeppie" and Helen-Mar Wheeler, "Linn." Jepson zealously guarded his personal privacy, often keeping his office door closed to intruders, and even totally disappearing from sight for long periods, his whereabouts not even known to the botany department secretary.

In the academic setting he assumed a formal persona. In his view most of his teaching colleagues were neither very qualified nor working hard enough, while he seemingly was working overly hard and being underappreciated. He was much better out in the field and had a faithful cadre of non-academic acquaintances, but in the field he might still appear in what we today would call somewhat formal attire, right down to a fedora with hat band, a white shirt with black tie, and a black vest, on occasion even a black suitcoat. He was, obviously, no longer the young collegian who had enjoyed dancing with Misses Spohn and Cora Smith and who, with classmate Wharff, sang with fervor, "So when a maiden kisses me, I'll think that I the Sultan be. . . ."

With respect to friends, an astute graduate student observed that Jepson had "at least 10 or probably 13 circles of friendships," with very few in the inner circle, especially among the faculty. One of Jepson's measures of friendship was complete loyalty to Jepson. For example, if a student or colleague gave plant specimens or attention to other than Jepson, the individual was quickly moved to an outer circle. Jepson himself admitted that he had a quick and violent temper, like his father, and it was readily directed towards those he came to dislike. Yet with the select few in that innermost circle the friendship was mutual and would continue for years. Surprisingly, there were few individuals, as his graduate students Herbert Mason and Lauramay Tinsley had observed, who actually disliked Jepson as much as he increasingly seemed to dislike others.

Despite the onset of the Great Depression, 1930 was a momentous year for the natural sciences at Berkeley, with the completion of the major Life Sciences Building at the lower end of the campus, the move commencing on January 5. Jepson should have been delighted. In the new building he had a beautiful office and a large private herbarium, situated next to a seminar room and the secretary's office. But after only the winter months on campus, Jepson was again afield, to the Kettleman Plains at the southwest end of the San Joaquin Valley in mid-April and back to Barstow and the Mohave Desert

for a week in early May. Then on May 21 he was off for another International Botanical Congress, this time in Cambridge, England, with a week at the Gray Herbarium and several days at the New York Botanical Garden before he took ship to Europe. Since the Congress didn't convene until mid-August, he inevitably spent most of the two intervening months at Kew. "It is a great delight to be here again," he wrote in his field book. "I feel a real thrill at being once more within the bounds of the Garden. The collections are so vast, so rich, apparently inexhaustible are the botanical treasures stored here. And one is given so kind a welcome by all the staff that it warms one." Jepson had once written that his favorite herbarium was his own in Berkeley, but his second fondest was the herbarium at Kew. Finally, with mid-August at hand, Jepson spent a short time in Oxford and then on to Cambridge University for the meetings, where he delivered a paper on "The Role of Fire in Relation to the Differentiation of Species in the Chaparral," and finally back to Kew. This time Jepson's return to America was by Montreal and across Canada to Vancover by train.

The next year Herbert Mason, who had essentially been Jepson's assistant since 1925 and whom Jepson viewed as an accomplished and loyal disciple, was appointed instructor, going on to teach the systematics course and supervising labs for Jepson. As time went by, Professor Jepson came to handle only a graduate seminar, for which he would pick a particular topic such as Age and Area, Life Zones, etc., the topics often remaining the same every time Jepson taught the seminar, a pattern which students were quick to recognize.

As Jepson frequently was absent for health reasons, Mason would periodically take over responsibility for Jepson's classes. Mason received his Ph.D. degree in 1932 with a thesis on the paleobotany of conifers and 2 years later assumed charge of the University Herbarium. Mason was a good and popular instructor, and he was an active participant in the departmental Calypso Club field trips, which is more than could be said for Jepson. Ultimately, in Jepson's view this up-and-coming young botanist was beginning to lure away Jepson's graduate students. And, indeed, he successfully did, starting with Carl Sharsmith. Furthermore, Jepson was incensed when Mason "took over" *Madroño,* which Jepson viewed as his own. Thus commenced an academic situation which would equal the Setchell-Jepson relationship, until at long last Jepson swore that he never even wanted to hear the name "Mason" mentioned in his presence; and indeed in Jepson's will it was emphatically emphasized that Mason not share in any of the benefits or endowments.

Meanwhile, in 1934 William Setchell, now a world authority on marine algae as well as being Jepson's enigma, retired, although he continued carrying on research for some time. As if in cele-

bration Willis purchased a new car, this time a very attractive sporty roadster that attracted excited attention wherever the professorial botanist drove. Jepson now had only 3 more years to retirement. He was the oldest member of the botany department and was not without fame himself, in America and in Europe as well. He might personally anticipate being named chairman of botany, at long last, or at least being consulted; but other pressures and personalities were abroad. A confidential committee of the university had recommended, once again, that botany be incorporated into the College of Agriculture. As a matter of fact, Dennis Hoagland, a plant nutrition authority, became chairman of the amalgamation of botany with the Division of Plant Nutrition. For Jepson, this was the ultimate treachery, with botany for the second time in his academic career losing its specific identity.

This mid-1930's period for Jepson came to rank with that terrible period in 1915. Worse now, in a sense, because he was older, much more taciturn and peevish, not in particularly good health, and increasingly driven by the necessity to complete the *Flora* before time ran out. Yet he was honored by the university with the prestigious invitation to deliver the University Research Lecture in Wheeler Auditorium on March 20, 1934. He entitled his address "The Content and Origin of the Californian Flora: A Demonstration of Scientific Methods," concluding with

. . . the joy of science is in never ending exploration and discovery and acquisition. I thought in the ardor of youth to build me a temple to my science. As I cleared the ground there in full view were the foundations of a previous temple, and under that the foundation of another and still others builded by the men who had gone before me. And in some parts the walls were sound, and in other parts only 'the ruined footings ran.' And I knew that in due time my temple too would be but as rubble and as ruin. As I thought of the future, of the far horizons that will open to view in the greater days to come, in the words of the great poet of Sussex, in his very words, I carved upon the lintel stone: 'After me, cometh a Builder, Tell him, I too have known.'

It was this year when the first edition of his *Shrubs & Flowers of the Redwood Region* was issued by the Save-the-Redwoods League, a popular publication still in print. Even amidst the Depression Jepson was receiving university research funds for his *Flora* work and was able to hire both artists and clerical help. As mentioned earlier, the second volume of the *Flora* would appear in 1936 (Capparidaceae to Cornaceae). Little could Jepson anticipate that the last part of his uncompleted *Flora* Vol. 4, Part 2, on the Rubiaceae, would be published in 1979 and would be written by Laura May Dempster, who had been not only one of his grad-

uate students but artist and personal assistant for the *Flora* into the 1940's. In the early fall of 1935, having been granted a 6-week leave of absence, Professor Jepson attended his last International Botanical Congress (the Sixth), this time in Amsterdam, with the usual stay at Kew Gardens. At the Congress he presented a paper on "Centers of Plant Endemism in California in Relation to Geological History." Back in Berkeley, just before Christmas, he was honored by delivering the keynote address for the University of California Forestry Alumni Dinner.

Jepson took delight in proclaiming that he was the only American to attend all of the International Botanical Congresses, but in truth he did not attend the First, in Genoa in 1892. True, he was in Europe in 1905, where the Second Congress took place in Vienna during June, but he didn't arrive there until July, and the meeting for which he was a delegate was an international congress for agricultural education. However, Jepson did take part in the Third, Fourth, Fifth, and Sixth, and he was an official delegate for the last two.

The academic year of 1936–1937 would be Jepson's final association as an active member of the University of California faculty, and his major voiced regret was that he was retiring just when he had encountered his two most talented graduate students, Robert Hoover and Joseph Ewan. Incidentally, Hoover received his Ph.D. in 1937 and actually worked as an assistant for Jepson until 1942. He was recognized by Jepson as "one of the ablest collectors in California. He had a trained eye for material of importance." Hoover would eventually go on to his own successful career in academia. Ewan, on the other hand, left for a teaching position at the University of Colorado and would never complete his Ph.D. But moving eventually to Tulane University, he pursued the subject of early American naturalists throughout his lifetime, something in which Jepson had interested him, eventually becoming an eminent historian of American natural history.

Willis had spent the summer of 1936 in his favorite redwood country of northwestern California. During autumn he taught his advanced graduate seminar. But after Christmas he was frequently in poor health, and was in and out of the sanitarium at St. Helena until the end of April, 1937, with Herbert Mason handling his classes. Then he recovered sufficiently to make a collecting trip to the Sierra around Jacksonville, and for several weeks in May back to the Mohave Desert and Barstow.

Although the academic year of 1936–1937 didn't end until August 19, the University granted Jepson a leave of absence from July 1 to that date. During the latter part of July, 1937, he drove north to visit two former graduate students, Helen Gilkey at Oregon State in Corvallis, and Lincoln Constance, who was on the faculty at Washington State, whom he warned not to take the offered position at Berke-

ley. Then on July 31, near Crescent City on his way home, Jepson stopped at a roadside spring to get a drink, caught his foot on a shrub branch, and seriously fractured his ankle. He went into the Knapp Hospital in Crescent City until August 18, and then was at the St. Helena Sanitarium until the end of September. This was not an enjoyable introduction to retirement, and to compound matters he had to have his immense herbarium moved down into the basement of his home on Mosswood, where it shortly began to suffer from insect attack.

Now no longer with academic obligations, Jepson was free to get into the field when he pleased, health permitting. He spent almost two weeks in April of 1938 in the northern Sierra, going up the Sacramento River Valley to the Red Bluff countryside in June after a May of intermittent botanizing in some of his favorite old haunts around Vacaville and the Napa Valley, with a brief stay at the sanitarium. Undoubtedly the high moment this particular year was when he was invited to deliver the banquet address for the Silver Jubilee of the California Botanical Society, which he, of course, had started; and his fitting though perhaps self-serving topic was the Society's beginning years.

Jepson had been involved on and off with Rancho Santa Ana Botanic Garden since 1926 when he supported its establishment. He consulted with Mrs. Bryant and her staff and became a councilor in 1933. During April of 1939 he combined a council meeting there with an extended collecting trip in southern California. In June he attended the American Association for the Advancement of Science (Pacific Section) meetings at Stanford, spending three weeks later in the summer up in the Feather River region of the northern Sierra. The next year his field schedule would have exhausted a botanist much younger than he when he spent almost a month afield in the Death Valley region, then three weeks in June and early July for a junket to Seattle for a AAAS meeting, driving up and back through the Sacramento Valley and central and western Washington. During October he was back at Rancho Santa Ana for another council meeting.

Jepson's last extended excursion of his career was during April of 1941, toward the end of his 74th year, although he would continue to take short field trips after that time. He had driven from Berkeley down to Rancho Santa Ana for another meeting of the Botanic Garden Council on April 19. But this time the meeting was a "peaceful" event for Jepson because he had "no duties, no obligations," and initially only the staff was aware that he would be present. But after Dr. Carl Wolf's public lecture on conifers in the auditorium, Jepson was absolutely delighted upon being recognized, because "a little procession of visitors lined up" to get his autograph.

He and Wolf had planned for an excursion after the Council to the Old Dad Mountains (actually the Granite Mountains) in the eastern Mohave, the pair

to meet for the trip at the Van Dyke Ranch in Daggett, which Jepson had often visited over the years. This was the ranch started by "Judge" Theodore Van Dyke, brother of the author of the classic *The Desert,* John C. Van Dyke. The Judge was a writer in his own right as well as Daggett's longtime justice of the peace. The Judge had died in 1923, and Jepson's host in 1941 was his son Dix, also a "desert writer." Still in residence at the ranch was Abby Waterman's friend Mary Beal, with whom Jepson first became acquainted during his prolonged stay in the Mohave three decades earlier. Suffering from tuberculosis, Mary, on the recommendation of John Muir (whose daughter Helen was recovering from the disease at the Van Dyke Ranch), had left her librarian job in Riverside and moved to the desert about 1911. Over the years Mary became an authority on the desert vegetation, photographing and writing about the flora, and was one of Jepson's prime collectors and collaborators. As he observed, she "knows every plant in her desert that has anything of popular interest."

Leaving Rancho Santa Ana, Jepson drove over Cajon Pass to Barstow, where he received the sad news that his old friend Abby Waterman had passed away just two days earlier, on April 19, in Berkeley. Continuing east to Daggett, Jepson reached the Van Dyke Ranch where sleeping quarters were found for him. At the ranch Mary Beal invited him to use the enclosed front porch of her cottage as his laboratory. Also, because Jepson had never been enthusiastic about the Dix cooking, Mary fed him his meals. The two took some local collecting trips, and back at the cottage Mary changed his plant driers, spreading damp specimens out in the sun. Meanwhile, Carl Wolf showed up on April 27, and he and Willis departed in Wolf's field vehicle for a thorough investigation of the Granite Mountains and the Kelso Dunes. This was Jepson's second desert excursion with Wolf, the two having been together during late April of 1935, when Jepson had been so impressed not only by this up-and-coming young Rancho Santa Ana botanist, who proved to be "a capital companion," but by the innumerable mounts for plant driers festooning the top and sides of Wolf's automobile.

It was on his return from this 1941 expedition that Jepson was invested by the University of California with an LL.D. degree, an honor which in part made up for what Jepson felt were years of neglect. However, when he was first told about the proposed honor, he actually wrote a letter (unsent), in essence declining the degree as an honor too late and too little. On December 7, 1941, of course, World War II commenced, which irritated Jepson on several scores. He lost his research assistants and research funds to the war effort, and as a staunch Republican he had to suffer under a Commander-in-Chief by the name of Franklin Delano Roosevelt.

During Willis Linn Jepson's last decade, his ob-

session with completing the *Flora,* now focusing on the demanding Scrophulariaceae-to-Compositae, was shared with a desire to elucidate his lifelong accomplishments. With a sense of manifest destiny, from his earliest days Jepson had felt a compulsion to save everything pertinent "as part of his life and autobiography"—his extensive correspondence, field notes, photographs, honors, mementos, passports, business cards, programs, rough drafts of articles, and so on. As he jokingly observed, "You would think . . . all this old stuff of mine were as valuable as pearls—real pearls!" Secretaries and assistants were busied organizing the correspondence, preparing letters so that they could be bound into volumes, which eventually would total 51 tomes, including a comprehensive index. Each bound volume includes 300–400 pages of epistles, with the total exceeding 15,000 items, all of which are now part of the Jepson Herbarium Library. In addition, there are reams of correspondence which have never been bound. The year before he died, Jepson perceptibly wrote with respect to this vast collection of correspondence that "Such a file will be, in the future, consulted by many persons and should be available to any one."

Some of Jepson's correspondents were remarkably faithful through the years. His Vacaville boyhood chum Ralph H. Platt sent chatty, homespun letters from 1888 until his death in 1928, often with a jocular salutation such as "Dear Billious." Equally delightful were the dozens of humorous letters and postcards between Jepson and Harry Dutton, a San Francisco businessman, Stanford graduate, and amateur botanist, between 1908 and 1945. The pair frequently greeted each other in correspondence with localities which they had visited: "Dear Vallecito," "Yours, Mission San Luis Rey." Willis Jepson's dearest relative throughout his adult life was his niece Dorris Pellet, daughter of his sister Mary and Frank Pellet of St. Helena. Dorris had a varied professional career in public service around the world, never married, and was considered a mirror image of her uncle in terms of personality, profile, and interests. Their letter writing extended over the years, and during Jepson's last few years Dorris wrote him lengthy epistles every Friday almost without fail. Not to be overlooked are the number of letters and notes starting in 1941 that went between Jepson and his latter-day unofficial "secretarial assistant," geneticist Helen-Mar Wheeler, whose father and Jepson had been on campus together as students. Helen-Mar would eventually become executrix of Jepson's estate.

With respect to Jepson's five dozen field books, he began going back over them, enhancing many of the entries from his remarkable though on occasion faulty memory, and he had compiled 20 additional volumes which brought together his notes on California botanical collectors (four volumes), observations on systematic botany, plant common names, field records, addresses of botanists and other individuals, three indices, etc. These, too, now make up part of the Jepson Herbarium Library collection.

He began penning a series of reminiscences on early Vacaville days for the Vacaville newspaper and continued to write articles on California's botanists, his last one on his old friend and lily enthusiast Carl Purdy being published after Jepson's death. But the book that he had long planned, *The History of Botanical Exploration in California,* would never be completed, nor the work on California plant geography, nor his booklet on plant common names, nor, fortunately, his many-chaptered, often venomous diatribe, "Man and Manners," which mixed "many delightful things in the manner of John Adams" with what Jepson caustically termed the "gangsterism" in academia. Other things, however, were being taken care of. As Jepson over the years had built up his herbarium, he had generally not put the plants on sheets, feeling that he and graduate students could make more successful use of them if they were loose. Now at last many of the specimens were being mounted.

Jepson began reflecting on his botanical collecting experiences throughout California and contemplated his favorite habitats. The White Fir belt of the Sierra Nevada had "a strong appeal," and the alpine slopes had a "strong grip" upon him. But better was the "magnificent" redwood country of the northwest. The deserts had "irresistible fascination" for Jepson and he came "back to them again and again," always regretting missing a fine season. But he had "no native affection for the desert ranges because of their ruthless implacable defiance." The Great Valley plains were "magnificent" but their immensity was overpowering. As he told fellow botanist Carl Wolf, "I like best the Coast Range valleys and their bounding ridges where still primitive or nearly so," from Lake County south to Parkfield, as well as the San Diego backcountry. The Vacaville foothills and St. Helena with nearby Mt. Howell had a special affection. At the bottom of his list was the ocean shore line, "the utter cruelty and hopelessness of the sea" depressing his spirit both with respect to collecting and traveling across the ocean aboard ship.

Inevitably, Jepson had early developed a perceptive ecological, as well as a biogeographical sense, resulting from his extensive field work in California and abroad, broadening experiences which many taxonomists of the day seemed to lack. As early as 1902 he contemplated taking up "a treatise on the plant geography of the state," and he actually did delineate major areas and even local plant communities such as those of spring ("vernal") pools. In his writing he frequently included ecological considerations. Collecting during July atop Mt. Lyell in Yosemite he noted that more plants were blooming on the summit than below on the north-facing slope. He made a point of saying that from an ecological standpoint the diversified flora of

Moraga Ridge, over the hills beyond Berkeley, was his favorite example.

Somewhat ahead of his time, a dozen small-type pages in the first section of Jepson's 1925 *Manual* dealt with an "Outline of Geographic Distribution of Seed Plants in California," discussing floral distribution related to Merriam's life zones, with a section devoted to "Irregularities in the Life-Zones," a consideration of plant distribution and geologic history, and several pages about "The Endemic Populations" with a map showing some endemism areas in California. And although Jepson had an antipathy towards introduced species, he included a section on "The Alien Populations." For comparison, in Abram's contemporary first *Flora* volume only three pages discussed such topics.

Jepson rightly chided American ecologists for paying too little attention to correct identification of plants, and he viewed with interest mixed with skepticism the increasing botanical interest in cytogenetics on the part of systematists, but rationalized that with the demands of completing the *Flora* he could not, despite his mild interest, afford the time at his age to become accomplished in this emerging botanical field. But Jepson did anticipate that eventually genetics would get around to consider all organisms, "and then we would really know how many there were." Professor Robert Ornduff, looking back on Jepson's accomplishments 40 years after his death, concluded that "I continue to marvel at Jepson's insights into matters just now being explored by botanists."

As mentioned earlier, Jepson had begun numbering his plant collections definitively in the year 1899. His professional career's last numbered specimen, No. 27,571, in his final field book, was, of all things, *Salsola kali* L. var. *tenuifolia* Tausch (*Salsola tragus* L.), collected at the Antioch Sandhills. The herbarium sheet is in the Jepson Herbarium, incorrectly dated November 11, 1945. In actuality, Helen-Mar Wheeler had driven Jepson to the sandhills on October 28. Later Rimo Bacigalupi had added the following note to the sheet: "This is the last specimen collected by Dr. W. L. Jepson." Yet even for this ignominious exotic weed Jepson not only penned a detailed description, as had often been his wont through the years for collected specimens, but added a sketch of the pistil and stamens. Jepson was in his 78th year. In mid-April of 1945 he had suffered a heart attack, overstrained by cutting down a dead almond tree at his Little Oak Ranch. He would never completely recover, spending much of his time in the sanitarium at St. Helena and later in a hospital in Alameda. Finally, on November 7, 1946, at his beloved home on Mosswood in Berkeley, Willis Linn Jepson passed away peacefully.

Dr. Jepson, that son of Vacaville pioneers, would express in his darker moments the fear that "one is always without honor in his own country." Yet Professor Jepson has been memorialized for the Jepson Herbarium, which now with more than 90,000 specimens celebrated its 50th anniversary in 2000, and for his diversity of publications, about 230 ranging from major books and scientific treatises to a three-page popular article in *Sunset Magazine* on "Where Ducks Dine," and indirectly including the new *Jepson Manual.* To Lincoln Constance, on one occasion, Jepson well expressed the obligatory relationship between plant collections and publishing: "It matters not how much knowledge may be accumulated about a given species, how many monographs discuss it—always botanists wish *to go back to the plant,* to authentic specimens. A flora which cites no specimens whatsoever may be a useful flora but it is not a scientific flora."

David Keck in his 1948 obituary for Jepson in *Madroño* tabulated who had named the largest number of California plant species by that time, and Jepson ranked number nine. Only one other erstwhile Californian outranked him, his mentor Edward Lee Greene, who had a reputation for generating scientific names. Speaking of appropriate names, there is the saxifrage genus *Jepsonia,* designated by John K. Small of the New York Botanical Garden. And the scientific names of innumerable species and subspecies of California plants honor Jepson, as well as those having been coined by him. Finally, although Jepson claimed he disliked the "folk names" for plants, he was always quick to point out the ones he had popularized. In fact, he once proudly claimed that "I have invented more common names of native plants for nonbotanists than any one else in the New World." Among his favorites were undoubtedly Mountain Misery (hike through it for miles and you'd appreciate why Jepson, as he emphasized, called it that), Johnny-tuck, and Red Maids, or "Kisses" as they were known in Sonoma County. Jepson named Johnny-tuck after an elderly hired man on the Little Oak Farm, whom he remembered as a child standing in a field of those flowers in his Sunday-going-to-meeting finery. When Jepson queried a little farm girl why she called Red Maids "Kisses," she shyly replied "You don't always *know* why, you just do!" Jepson, by the way, was quick to chide authors who published his common names without crediting the source, yet he didn't seem concerned that the country folk who gave him many of his names seldom received any specific recognition from him.

At the western edge of his boyhood town there now stands the Willis Jepson Middle School, dedicated on May 23, 1960, with appropriate floral plantings and colorful mural, bordered by streets named Jepson Way and Jepson Court. At Tomales Bay State Park there is the Jepson Trail, leading to the Willis Linn Jepson Memorial Grove of Bishop Pines, dedicated on November 8, 1952. There is a Jepson preserve on the Klamath River in northern California, one of his collecting haunts, and the Jepson Prairie in the Suisun Marsh country, another

Jepson botanizing locale. In 1902 it was Jepson who discovered the world's largest Coast Madrone (now recently fallen) in Humboldt County and named it the Council Madrone, after coast and interior Native American tribes that used to parlay there. Two years later, Jepson planted a redwood beside the Vacaville cottage into which his mother moved from Little Oak Ranch after her husband's death, and that redwood now towers over the cottage in this new century. Jepson would serve on the Council of Save-the-Redwoods League from its establishment until his death. He was also the honorary vice-president of the Sierra Club the last five years of his life. On April 15, 1923, members of the California Botanical Society gathered near Lower Crystal Valley Reservoir south of Millbrae to dedicate California's second largest Bay Tree as the Jepson Laurel.

In 1972, a quarter of a century after Willis Jepson's death, the United States Geological Survey designated a jagged 13,390-foot wilderness peak as Mt. Jepson, in King's Canyon National Park near Mt. Whitney and close to Willis Jepson's old Sierra Club hiking route. In silhouette Mt. Jepson, rising dramatically far above timberline beyond a U-shaped glacial gorge, remarkably resembles the distant skyline peak portrayed in Jepson's book plate, with its inscription "Something lost behind the ranges—over yonder—Go you there." This appropriate alpine monument in the high Sierra would indeed have pleased "The Botany Man."

Literature Cited

This biographical treatise on Willis Linn Jepson is based upon an extensive variety of original primary and a limited number of secondary sources, the most important of the former being the volumes of Jepson Correspondence, Jepson Field Books, and the Jepson/Helen-Mar Wheeler Collection, all in the University of California Jepson Herbarium Archives, with other valuable sources including the various published obituaries of Jepson, and the oral interviews with Laura May Dempster, Joseph Ewan, and Lincoln Constance in the Jepson Archives. Minor points of clarification were derived from a number of published books and articles, but most quotations are from original documents at the Jepson Herbarium Archives.

PRESIDENT'S REPORT FOR VOLUME 47

As the California Botanical Society's program year draws to a close, I have the pleasure of reviewing this year's accomplishments and activities. I also take this opportunity to thank the officers and council members for their dedicated efforts to keep the Society a vital force in west American botany. On behalf of the Society, I offer special thanks to Editor Kristina Schierenbeck for her continuing progress toward bringing *Madroño* back onto publication schedule and elevating further the stature of the journal. I am delighted to announce that Kristina has very generously agreed to extend her invaluable service as Editor of *Madroño* for a fourth year, through Volume 48. We are now searching for a new Editor of *Madroño,* for Volumes 49–51, and I encourage an aspiring editor to contact me or Kristina soon so that we can begin planning for a smooth transition.

Incoming First Vice-President Rodney Myatt helped the Society off to a strong start in fall 2000 by organizing an outstanding slate of speakers for our monthly meetings at U.C. Berkeley. We heard excellent presentations by John Battles, Chris Brinegar, Tina Carlsen, Susan Harrison, Dan Norris, Dan Potter, and Maureen Stanton on a wide range of botanical subjects, each followed by a post-seminar reception in the University and Jepson Herbaria. Many thanks to Rodney for his excellent planning and to our graduate student representative, Kirsten Johannes, for faithfully coordinating the invitations and receptions for each of our monthly meetings during the past year.

On 17 Feb 2001, the Society held one of its most important functions, the biennial graduate student scientific meeting, in conjunction with the annual banquet. The two events were held this year on the campus of the California State University at Chico. The graduate student meeting, organized by Chico graduate student representative Leah Mahan and CBS graduate student representative Kirsten Johannes, was by all accounts a great success, and both of these hard-working students deserve thanks and congratulations. Scientific papers on proposed, ongoing, and completed botanical research were presented throughout the morning and afternoon by 35 student speakers from within and outside California. Graduate student research is responsible for much of what we know about west American botany and I highly recommend regularly attending this highly educational event.

Second Vice-President Rob Schlising did an excellent job of hosting the Society's well-attended 2000–2001 annual banquet. Past President Wayne Ferren graciously stepped in to officiate over the evening's events while I was fighting off a flu in Berkeley (thank you, Rob and Wayne!). Attendees of this year's annual banquet were treated to an after-dinner lecture by Professor Emeritus Arthur Kruckeberg (University of Washington), the premier authority on serpentine endemism in plants, on the role of geology in molding the California flora. On behalf of the Society, I thank Dr. Kruckeberg for making this year's banquet such a special and memorable occasion.

A priority of the Council during the past year has been to elevate visibility and membership of the Society and, especially, to increase circulation of *Madroño* and citation of articles therein. Inclusion of *Madroño* in BIOSIS has been a positive step toward increasing article citation and we are actively pursuing incorporation of *Madroño* into other on-line databases. Thanks to incoming Society webmasters Curtis Clark and John LaDuke, the California Botanical Society now has an active and attractive web-site (www.calbotsoc.org), which will soon include abstracts of *Madroño* articles (beginning with Volume 48) and should help to alert more botanists to the value of *Madroño* and membership in CBS. Recording Secretary Dean Kelch spearheaded a membership drive during the past year that resulted in wide dissemination of information about the Society (and *Madroño* in particular) to academic and agency plant scientists throughout the West. I thank Dean and the other members of the Council for their important help in the membership drive. I ask all members of the Society to help promote our membership by encouraging your non-member collegues to join us.

Two hard-working members of the Council that deserve special thanks for their efforts to ensure continuity of the Society's membership and general maintenance of the Society's finances are incoming Treasurer Roy Buck and Corresponding Secretary Susan Bainbridge. Thanks in part to Roy's and Sue's conscientiousness, the Society's membership base is growing. I also thank Council members Diane Elam, Jim Shevock, and Bian Tan for their thoughtful contributions toward helping to chart the future of the Society and Recording Secretary Dean Kelch for reliably keeping minutes of our monthly Council meetings.

Of course, none of our activities would be possible without the contributions of the members of the California Botanical Society. On behalf of the Council, I thank each of you for your critical support of the Society's important goals and look forward to your participation in our new program year!

—Bruce G. Baldwin. July 2001.

Editor's Report for Volume 47

This report serves to inform members of the California Botanical Society the status of *Madroño* from manuscripts submitted to papers published. Since the previous editor's report (see *Madroño* 46[4]) the journal received 73 manuscripts for review, including Articles, Notes, and Noteworthy Collections; 64 of these have since been accepted for publication. The average time from article submission to publication has been remained stable at approximately six months. Very few manuscripts were rejected after review. Authors of *Madroño* articles are generally quite responsive to reviewer and editorial suggestions.

The publication schedule has been returning, albeit slowly, to a regular publication schedule. We are currently within six months of returning the journal to an on-time schedule, as publication submissions have increased in frequency. Noteworthy collections continue to be a valuable contribution to the journal but have suffered from reduced attention due to editorial efforts with other manuscripts.

There are many individuals who contribute to the editorial process; Jon Keeley, who continues to serve as book review editor; Steve Timbrook, who continues to assemble the Index and Table of Contents; Dieter Wilken and Margriet Wetherwax, who edit the Noteworthy Collections; David Parks and Jeannie Trizzino, my editorial assistants; Michael Abruzzo, Chair of the Department of Biological Sciences at California State University Chico, who provides the funds to support David; Karen Ridgway at Allen Press; and members of the CBS executive council who enthusiastically support *Madroño* in every aspect. I continue to rely on the council of Robert Patterson, Wayne Ferren, Jon Keeley, John Strother, and Beth Painter for guidance about the editorial process. On behalf of the society, I thank the volunteer reviewers and the Board of Editors on whom we all depend to make the peer review process work for this valuable regional journal.

Reviewers of Madroño Manuscripts 2000

James Agee
Geraldine Allen
Ihsan Al-Shehbaz
Michael Barbour
Theodore Barkley
Matthew Beaty
Bruce A. Bohm
Lynn Bohs
Kenneth Cameron
Curtis Clark
Kenneth Cole
J. Travis Columbus
Steve Darbyshire
Frank Davis
Richard S. Dodd
Aron Fazekas
Wayne Ferren
Bruce Ford
John Freudenstein
Candice Galen
Barbara Gartner
Carol Goodwillie
Craig W. Greene
Howard Griffiths
F. Thomas Griggs

James Hamrick
Gary Hannan
Klaus Helenurm
Noel Holmgren
Sara Hoot
David C. Jarrell
Leigh Johnson
Steve Junak
Jon Keeley
David Keil
Elizabeth Kellogg
Job Kuijt
John LaDuke
David Lemke
Yan Linhart
Aaron Liston
Timothy Lowry
Scott Martens
Robert Mathiasen
Steve McLaughlin
John McNeill
Kathy Merrifield
Richard Minnich
Brent Mishler

James Morefield
Guy Nesom
Steven O'Kane
V. Thomas Parker
Robert Patterson
Mark Porter
James Pushnik
James Reveal
Ronald Robberecht
Gregory Saenz
John O. Sawyer
Rob Schlising
Joanna Schultz
James Shevock
Scott Stephens
Nathan Stephensen
Michael Stieber
Robert Stockhouse
John Strother
Stanley Welch
Dieter Wilken
Paul Wilson
David Wood
Frederick Zechman

INDEX TO VOLUME 47

Classified entries: major subjects, key words, and results; botanical names (new names are in *boldface*); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

ROBERT ORNDUFF

1932–2000

Dr. Robert Ornduff, Professor Emeritus at the University of California, Berkeley, died on September 22, 2000, at the age of sixty-eight, in Berkeley from complications of metastatic melanoma. "Bob was one of the treasures of the botanical world, a green-thumb botanist who delighted in growing plants and disseminating his interest to the general public. He was a 'rara avis' in botany these days, who could operate brilliantly in both natural history and in 'ivory tower' plant biosystematics," according to Art Kruckeberg, professor emeritus at the University of Washington, Seattle, Bob's mentor and friend. Bob's distinguished career spanned some thirty-seven years at the university. He leaves an impressive legacy of research in plant evolutionary biology, of mentoring highly distinguished students, of major contributions to the development of the University Botanical Garden, and of a lifetime of effective participation in the botanic community outside the university.

Born in Portland, Oregon, on June 13, 1932, Ornduff grew up in the suburbs near a golf course, where he collected and took home to raise numerous found creatures such as giant Pacific salamanders, fish, snails, and baby birds, a habit he retained throughout his life. Following graduation from Washington High School in Portland, he attended nearby Reed College and graduated in 1953 with a major in biology. Bob next obtained a Master's degree at the University of Washington (1956) studying under the direction of Art Kruckeberg. He had met Art four years earlier, when Art was an instructor in a nine-week University of Washington summer field course, and the two developed a lifelong friendship. Bob claimed that, while he knew from childhood that he wanted to be a biologist, it was Art who drew him into a career in botany. During his studies with Art, he received a Fulbright scholarship and spent a year in New Zealand, looking at the distribution and systematics of the puzzling and polymorphic New Zealand *Senecio lautus* complex. Kruckeberg commented that "His study of the group was certainly Ph.D. worthy in quality and extent. It was later published in a New Zealand journal."

In 1955, Bob moved to the University of California, Berkeley, commencing studies for his Ph.D. degree. One of us (PR) met him there as a Berkeley undergraduate, and commenced a lifetime friendship. Like many other Berkeley students, Bob was greatly influenced by Herbert Mason's course in plant systematics, an outstanding inquiry-oriented course in which Don Stone was the teaching assistant and Job Kuijt, Galen Smith, Howard Arnott, Jean Langenheim, and Peter Raven were among the fellow students. Evidence of all kinds for arriving at a proper understanding of plant classification and evolution was considered in discussions. Field trips, hours of discussion and analysis, and good companionship made the course a memorable learning experience for all who were associated with it. Bob commenced his graduate studies under the direction of Professor Mason, taking a year out to fill in at Reed College, and obtained his degree in 1961.

During Mason's course, one of us (PR) suggested that the group of composites known then as *Baeria* might be an interesting subject for Bob's dissertation research. Earlier, K. L. Chambers had found different base chromosome numbers within the genus, and it seemed likely to be a suitable subject for biosystematic inquiry. Bob's thorough investigation of the genetics, morphology, ecology, and evolutionary relationships resulted in the realignment of generic limits and the incorporation of *Baeria* into the genus *Lasthenia,* with many interesting relationships revealed in the course of the study. The taxonomic treatment resulting from his dissertation (1961) was published by the University Press as a monograph, *A Biosystematic Survey of the Goldfield Genus* Lasthenia, in 1966. After applying various approaches to the further elaboration of evolutionary relationships within *Lasthenia* over the years, Bob took particular delight in the work of Raymund Chan, his last graduate student, who is using molecular systematic to deepen our understanding of the genus *Lasthenia.* These studies have also resulted in the recognition of a new species of *Lasthenia,* which Raymund intends "to name in memory of Dr. Ornduff."

Bob Ornduff's first academic position after his graduation was at Duke University (1961–1963), but when invited to fill Mason's chair at U.C. Berkeley found the offer to be irresistible. At his alma mater he served with distinction in a number of capacities: director of the Jepson and University Herbaria from 1967 to 1982, director of the University Botanical Garden from 1973 to 1991, and chairman of the Botany Department from 1986 to 1989, when it merged into the Department of Integrative Biology. He served as chairman of the Editorial Committee at the University of California Press from 1975 to 1989, during the years when August Frugé was director and then for a requested holdover year when Jim Clark became director. Bob was executive director of the Miller Institute for Basic Research in Science from 1984 to 1987,
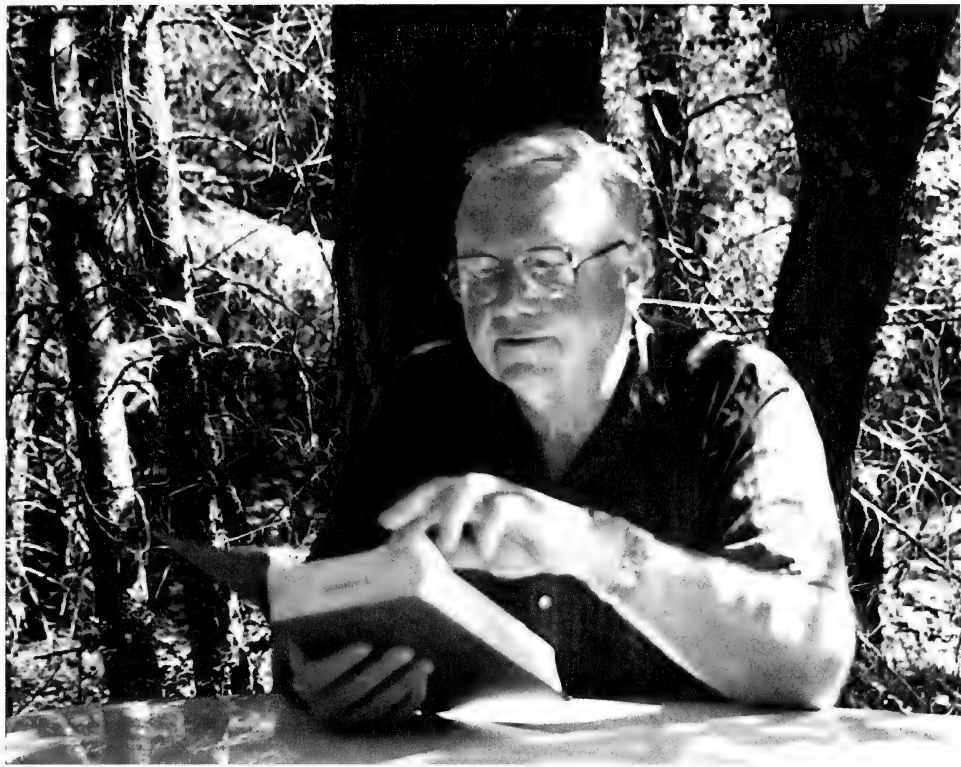
Fig. 1.   Dr. Robert Ornduff botanizing at New Anguin, May 1989. Photo by Ken Wilson.

a program that awards grants both to visiting investigators and students and to campus faculty for work off-campus. At the time of his death, Ornduff was actively involved with Jepson Herbarium, the University Botanical Garden, and his own research on the population dynamics of the genus *Villarsia* (Menyanthaceae). He also was co-editor of the Natural History Series at the University of California Press with one of us (PF).

Ornduff wrote more than 100 scientific papers and over 50 less formal papers on horticultural and related topics. He edited two books and wrote one, the popular *Introduction to California Plant Life* (U.C. Press 1974), which is still in print and has introduced generations of students to California's unique flora. Following his retirement in 1993, he continued teaching his popular California Plant Life course through the U.C. Extension program to many hundreds of students.

Ornduff's research interests were broad but in general focused on the evolution of species and species diversity. According to Steve Weller (now a professor in the Department of Ecology and Evolutionary Biology at U.C. Irvine), "Bob was one of the first bridges from biosystematics and evolutionary biology to plant population biology and was an inspiration to many." A seminal event in Bob's research career was his discovery of the unique fall-blooming saxifragaceous genus *Jepsonia* while on a field trip in 1956. He soon realized that *Jep-*

sonia was heterostylous, where some individuals bore flowers that had long styles and short stamens (pin), and others had the opposite condition (thrum). *Jepsonia* comprises three species, confined to small areas of California, adjacent Mexico, and the offshore islands. In 1961, Ornduff published his first paper on the genus, reporting heterostyly in it and in the family Saxifragaceae for the first time. Thus he began a lifelong fascination with heterostyly and its relationship with dioecism, investigating the phenomenon in several other groups including *Oxalis* (Oxalidaceae), *Pontederia* (Pontederiaceae), *Lythrum* (Lythraceae), *Hypericum* (Guttiferae), *Leucocrinum* (Liliaceae), *Villarsia* (Menyanthaceae), and *Amsinckia* (Boraginaceae). For *Nymphoides* (Menyanthaceae), he published evidence that heterostyly has been replaced by dioecism and analyzed the selective forces involved.

Ornduff was also interested in the population dynamics resulting from isolation and edaphic conditions. Early on in his career, in 1961, he visited the Farallon Islands off the California coast, where the sparse soil developed largely from seabird guano, publishing a florula of South Farallon Island. In 1981, he visited several granite rock outcrops in Western Australia (likely ones that Darwin had visited) and identified them as "islands in a sea of *Eucalyptus,*" analyzing their endemic plants. He returned in 1983 to undertake floristic studies that were later published and described in the Harold L.

Fig. 2. Dr. Robert Ornduff at his retirement party as Director of the University of California Botanical Garden, 1991. Photo courtesy of the U.C. Botanical Garden.

Lyon Arboretum Lecture Series and publications at the University of Hawaii. His papers are lucidly written and often pose interesting questions for further research.

Notable in Bob Ornduff's career was his work with graduate students. Two students, Steve Weller (University of California, Irvine) and Spencer Barrett (University of Toronto), fondly remember field trips with Bob to see his beloved *Jepsonia* populations in the Sierra Nevada foothills. They describe riding in his sleek Mercedes-Benz sports car accompanied by a gallon of "fine red wine." Spencer writes, "Bob always combined the best of botany with the gourmet delights of a field picnic in the finest style. This was one of the most important lessons I learned from him." Steve writes, "This trip highlighted Bob's love for the California landscape, his unerring ability to find interesting plants and research projects, and his generosity in sharing this with his students."

Former graduate student Jim Eckenwalder, now Associate Professor at the University of Toronto, provided a synopsis of Bob's approach to supervising graduate students. "In contrast to the increasingly common practice of slotting Ph.D. students into an established program, Bob was a hands-off supervisor who encouraged our independence as scientists from the start. Even so he was always there for you when you needed him (at least when he wasn't doing fieldwork in some exotic locale). Most importantly, he never dropped his standards and always provided effective and instructive criticism, whether of the thesis, manuscripts, or oral presentations. Most of us worked on projects beyond his immediate area of interest, so his well honed and sometimes devastatingly sharp critical faculties were for us his greatest legacy. Mentor and friend, I will sorely miss 'Our O.'"

Doug James (currently the owner of a small micropropagating facility in Berkeley), longtime friend and three-time teaching assistant for Ornduff's California Plant Life course (Botany 125) in the 1970's recalls what a pleasure it was to be a teaching assistant for this class as Bob was such an extraordinarily good teacher. "Although majors would take his courses, he got supreme joy illuminating the subject for neophytes. . . . He never missed an opportunity to expand a discussion with examples from his own experiences or observations in the field. He made the subject come alive for his students."

For eighteen years from 1973 to 1991, Ornduff was director of the University Botanical Garden in Strawberry Canyon, Berkeley. His association with the garden brought him some of his greatest pleasures because of his lifelong interest in the diversity of plants and in cultivating them. He collected seed wherever he traveled and greatly enriched the collections in the garden in this way. Visiting the other four areas of the world with mediterranean climates, the Mediterranean itself, Western Australia, Chile, and South Africa, often with his close friend Bill Culberson, Bob built substantial living collections from each of them. Holly Forbes, curator at the garden, reports that Bob donated over 1100 collections from twenty-three countries, with over 700 still growing there. As Steve Weller, a former graduate student, observed "Bob's accessions for the garden were remarkable in their number and diversity. Certainly, it is hard to imagine a more interesting botanical garden during the era when he was contributing to the development of the collections. It was a labor of love for him, and he had a lifelong commitment to the garden, long after he ceased to be director."

His successful development of a "Friends of the Garden" docent program, however, perhaps provided Bob the greatest satisfaction. In an interview shortly before his death he commented that the Friends program's growth and evolution was one of his greatest pleasures. He liked getting to know people in the community, had a great admiration for many of the people in the program, and thought the docent program was "superb." As a result of his efforts, the Garden gradually increased its size and scope, and became a world-class collection of

plants from California and beyond. In recommending Ornduff for an Award of Merit by the Botanical Society of America (given in 1993), Sherwin Carlquist, a long-time friend and research botanist at the Santa Barbara Botanic Garden, commented that even though small in size, the University Botanical Garden "is, without a doubt, the most significant botanical garden in the United States, acre for acre, when compared to other gardens."

In 1992, Ornduff became director of the American branch of the Stanley Smith Horticultural Trust, a charitable foundation with a sister branch in Britain, both providing support for education and research in horticulture in botanical gardens, arboreta, and related institutions. He held this position until his death, refining the Trust's focus to include small gardens as well as great ones and thereby helping many fledgling operations establish viable programs. Unlike many professional botanists who shun association with horticulture, Ornduff always sought it out as yet another expression of his love of plants.

With his ready wit and humor and profound knowledge of the California flora, Bob was a popular speaker at garden clubs, California Native Plant Society meetings, and campus events. He last spoke at the 50th Anniversary Jepson Symposium banquet in June, 2000 with his lively talk entitled "Piss and Vinegar: Some Early California Botanists." As a founding board member of the California Native Plant Society, he played an important role in the formation of the organization by serving as vice-president from 1969 to 1971, and president from 1972 to 1973 in the era before chapters were formed. From 1971 to 1975 he was chairman of the editorial committee that produced the CNPS newsletter and founded its journal. Bob's proposed name for the journal, *Fremontia,* won a naming contest and for twenty-seven years (ten years for Marge Hayakawa and seventeen for Faber) he reviewed and commented on almost all submitted manuscripts for the journal. As editor, one of us (PF) was always profoundly grateful for his fast turnaround of material and quick eye for plant names. Steve Weller commented on the same quality. "He was a wonderful editor, and read everything I wrote within twenty-four hours!"

Ornduff received numerous honors for his work and contributions, among them: Award of Merit from the American Association of Botanical Gardens and Arboreta (1993); Merit Award from the Botanical Society of America (1993); F. Owen Pearce Award of Horticulture, Strybing Arboretum Society (1994); Fellow, American Association for the Advancement of Science (1966); Fellow, California Academy of Sciences (1967); Fellow, California Native Plant Society (1997); and member of the team that prepared the master plan for the San Luis Obispo Botanical Garden, which received a 1999 Merit Award of Planning from the American Society of Landscape Architects.

Bob Ornduff had a remarkably full career doing what he loved best, being closely associated with plants in many diverse ways. He arrived at his office at the university at around six a.m. "because he liked being there." His weekends were spent at his house in Inverness, for him a haven from which he explored the Point Reyes Peninsula from such places as an old limestone kiln in the Olema Valley to his favorite view of Ten Mile Beach near the lighthouse. He regularly kept track of the vegetative recovery beyond his house from the 1995 Mt. Vision fire and wrote on the subject twice. He liked picking huckleberries for jam and collecting apples from his own orchard for pies. For Bob, all plants had stories he enjoyed sharing. He collected myriad books about plants, and maintained friendships with botanists from many places around the world. His was a life devoted to championing, better understanding, and enjoying the world of plants.

—PHYLLIS M. FABER, University of California Press, Berkeley and PETER H. RAVEN, Missouri Botanical Garden, St. Louis.

Robert Ornduff
Curriculum Vitae

Born June 13, 1932, Portland, Oregon.

Educational Background

B.A. Reed College, 1953 (Biology).
Fulbright Scholar, Victoria University, Wellington, New Zealand, 1954 (Botany).
M.Sc. University of Washington, 1956 (Botany).
Ph.D. University of California, Berkeley, 1961 (Botany).

Professional Experience

Reed College: Assistant Professor, Biology, 1961–1962.
Duke University: Assistant Professor, Botany, 1962–1963.
University of California at Berkeley, Botany:
　　Assistant Professor, Botany, 1963–1966
　　Associate Professor 1966–1969
　　Professor 1969–1993
　　Professor Emeritus 1993–2001
　　Assistant Curator of Seed Plants, University Herbarium, 1965–1966
　　Associate Curator, University Herbarium, 1966–1969
　　Curator, University Herbarium, 1969–1993
　　Director, University Herbarium, 1967–1982
　　Director, Jepson Herbarium and Library, 1968–1982
　　Director, University Botanical Garden 1973–1991
　　Faculty Curator, 1991–2001
　　Chairman, Department of Botany, 1986–1989

Professional Service

President, American Society of Plant Taxonomists, 1975

Chairman, Editorial Committee, University of California Press, 1975–1989

Associate Editor, Evolution, 1975–1977

Council member, Society for the Study of Evolution, 1977–1979

Membership Committee, American Society of Naturalists, 1978–1979

President, California Botanical Society, 1981–1982

Executive Director, Miller Institute for Basic Research in Science, 1984–1987

Program Committee, Society for Economic Botany, 1987–1988

Board of Councilors, Save-the-Redwoods League, 1988–2001

Board of Directors, Pacific Horticultural Foundation, 1992–2001

Grants Director, The Stanley Smith Horticultural Trust. 1992–2001

Editorial Advisor, Fremontia, 1997–2001

Board of Trustees, Center for Plant Conservation, 1997–2001

Awards and Honors

Award of Merit, American Association of Botanical Gardens and Arboreta, 1993

Merit Award, Botanical Society of America, 1993

F. Owen Pearce Award of Horticulture, Strybing Arboretum Society, 1994

Fellow, California Native Plant Society, 1997

Author of over 100 scientific papers and about 50 papers on various horticultural and related topics.

Publications

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1966. The goldfield genus *Lasthenia* (Compositae: Helenieae): a biosystematic survey. University of California Publications in Botany 40: 1–92.

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1968. Numerical taxonomy of Limnanthaceae. American Journal of Botany 55:173–182. [With T. J. Crovello.]

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A CATALOGUE OF MOSSES FOR THE CITY AND COUNTY OF SAN FRANCISCO, CALIFORNIA

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ABSTRACT

The moss component for the bryoflora for the City and County of San Francisco contains 128 species representing over 22 percent of the California moss flora. Several mosses are suspected as being introduced since the mid-1900s and have subsequently become established and naturalized. A large component of the moss flora of San Francisco represents cosmopolitan species having wide geographical distributions. All but twelve of the 42 species based on the historic Bolander moss collections attributed to San Francisco from the 1860s were relocated during this study. Sixty-five mosses are reported for the first time from the City and County of San Francisco. Of these, the rare species *Triquetrella californica* (Lesq.) Grout is also documented for San Francisco. *Bryum pyriferum* Crundw. & H. Whiteh., *Campylopus pyriformis* (F. Schultz) Bridel, *Heterocladium dimorphum* (Brid.) Schimp. in B.S.G., *Sematophyllum adnatum* (Michaux) Britton and *Zygodon menziesii* (Schwaegr.) Arnott are reported new for California and *Zygodon menziesii* is reported new for North America.

What is today the city of San Francisco began at Mission Dolores when Spanish priests and soldiers established a mission on June 29, 1776. Since the California gold rush of 1849, San Francisco has functioned as a center for immigration, a focal point of commerce and as a financial center. Botanists too generally entered California via San Francisco (Slack 1993). Surrounded on three sides by the Pacific Ocean and San Francisco Bay, the City and County of San Francisco is contained at the tip of the San Francisco Peninsula, a compact rectangular area of 128 sq. km. (47 sq. mi.). Built on 43 hills, the City and County elevation ranges from sea level to 282.5 m. (927 ft.) at the summit of Mt. Davidson. Twin Peaks at 281 m. and 275 m. along with Mt. Sutro at 277 m. are the highest points near the geographic center of the City and County of San Francisco. With a population of 770,000, San Francisco is the second most densely populated American city after New York. The Bay Area metropolitan area is the Nation's fifth largest and the workday population of San Francisco swells to over 1.5 million (San Francisco Convention and Tourism Bureau).

During the past 150 years San Francisco has undergone phenomenal development with an associated loss of native habitats (Eastwood 1945, Howell 1934 and Howell, Raven & Rubtzoff 1958). As early as 1891, these landscape changes were already evident. In her introduction to the flora of San Francisco, Brandegee (1891) states "that the number of plants is not greater is due not only to the destruction of native species, caused by the cutting down of hills, filling of swamps and burying streams incident to the growth of a large city, but even more to the lack of variety in climate and conditions, the city being surrounded on three sides by water and swept by ocean winds." While several portions of the City and County remained undeveloped up until the 1940s, it was in the aftermath of WW II that many natural wild areas were rapidly developed for residential use in San Francisco (Howell, Raven & Rubtzoff 1958). While much of the original landscape was altered or converted to residential and high rise office buildings in subsequent decades, the City and County of San Francisco nonetheless still contain several areas of open space from landscaped parks to undeveloped hills where remnants of native vegetation still persist. In other areas, non-native plantations dominated by *Eucalyptus globulus* Labill. and *Cupressus macrocarpa* Gordon (although the latter is native to other coastal areas of California) contributed to the replacement of the natural vegetation. These plantations, now approaching 100 years old, provide many microhabitats for the establishment of moss populations.

History of moss collecting in San Francisco. Yerba Buena (the earlier name for San Francisco), was the northernmost expansion of Spanish rule in North America. There appear to be no moss collections obtained during the Spanish era between 1776 and 1821. Neither were moss collections made during the Mexican period from 1821 to 1846 when the United States declared war on Mexico. Yerba Buena was renamed San Francisco in 1847 and Alta California was transferred by treaty from Mexico to the United States in 1848. California was admitted to the Union as the 31st state in 1850. Moss collecting in San Francisco apparently began in the 1860s when Brewer collected *Bryum argenteum* near Mission Dolores in 1862, Kellogg collected *Alsia californica* from Lone Mountain in 1866 and Bolander collected several mosses at Mission Dolores and Fort Point in 1868. Earlier collectors of mosses in California include Sullivant in

1853 and Lesquereux in 1865 but label data are absent to conclude that any of their collections were obtained from San Francisco (Thiers & Emory 1992). Bolander, who was employed for a short time as a botanical assistant for the State Geological Survey, was the principal collector of mosses in California in the 1860s. His collections added significantly to the catalogue of mosses known from California (Lesquereux 1868 & Watson 1880), now evident in several taxa named to commemorate him.

Brandegee (1891) consolidated the Bolander collections housed at the University Herbarium, University of California and added a list of mosses to her San Francisco vascular plant flora. The moss flora was based on species concepts of that time and comprised 42 taxa. Bolander's label information, although standard for that era, was very sparse. It is difficult to determine exactly where many of the San Francisco specimens were obtained beyond the few references to Mission Dolores and Fort Point. There appears to be no published record to indicate the level of effort Bolander invested in his moss collecting endeavors within San Francisco.

In addition to these early field workers, several other botanists, known nearly exclusively for their flowering plant collecting and floristic publications, also collected mosses in San Francisco during their careers. Collections were made by Alice Eastwood in 1923, by Peter Raven in 1949, 1950 and 1954, by Frederick J. Hermann in 1962 and by John Thomas Howell in 1969. Among Peter Raven's first botanical collections were mosses obtained from Golden Gate Park when he was fourteen years old which he brought to the Academy of Sciences. Leo Koch and Fay MacFadden, the prominent field bryologists during this period, identified them.

We undertook this study to determine how many of the mosses obtained by Bolander, as reported by Brandegee (1891), Lesquereux (1868), and Watson (1880), and from subsequent collectors, could be re-located within the City and County of San Francisco after 130 years of substantial land-use changes. We also wanted to know if we could document mosses that were overlooked by Bolander and subsequent collectors and determine if additional mosses, such as introduced exotics, are now becoming a naturalized component of the bryoflora of California. Our field collecting began in the fall of 1999 and concluded in the fall of 2000. Together we obtained 668 moss collections representing 112 species within the City and County of San Francisco. Sixteen taxa reported by earlier collectors from San Francisco were not relocated during this study. Of this total, twelve were Bolander collections dating from 1868. We believe that potential habitat still remains within the City and County for most of these taxa, even though we did not encounter them during our study. Five of these taxa are soil ephemerals that can be easily overlooked. Only

three species, *Fontinalis neomexicana*, *Orthotrichum rivulare* and *Pohlia wahlenbergii* appear to be extirpated from the City and County of San Francisco through loss of suitable habitat. Several mosses were routinely encountered on a variety of habitats and substrates while others appear to be locally uncommon or restricted. The number of collections cited for each species is a good approximation of whether it is a common or a rare component of the moss flora in the City and County of San Francisco.

Fragmentation of habitats and associated substrates available for moss establishment. Today, remnants of free-flowing creeks and fragments of native vegetation ranging from sand dunes and northern coastal scrub to serpentine grasslands can still be found in San Francisco. Salt and fresh water marshes have been drained and filled decades ago but are beginning to re-establish on fill land. In the areas where small lakes (ponds) remain, the natural flow of water has been altered along with great changes in water chemistry. Most of these bodies of water are no longer viable for the establishment of mosses, primarily a result of algal concentrations and/or presence of pollutants such as those in storm run-off from streets. Nearly all of the forested habitat is the result of tree plantations or trees that became established and spread from initial plantings that date from the 1870s to the 1920s (McClintock & Moore 1965).

Several city parks are located throughout the City and County. The largest is Golden Gate Park at 407.5 hectares (1007 ac.). The Presidio and Golden Gate National Recreation Area, managed by the National Park Service provides a federal contribution to open space in the City and County of San Francisco. The most protected landscape within the County of San Francisco is the Farallon Islands National Wildlife Refuge, managed by the U.S. Fish & Wildlife Service. These isolated, barren, windswept granitic islands are home to thousands of breeding oceanic birds and pinnipeds and are closed to public access. Today several conservation efforts are ongoing to either maintain or restore native plant habitats from sand dunes and northern coastal scrub to serpentine grasslands. Management for endangered species is a catalyst for these various restoration efforts in San Francisco. Public debate will also focus on the long-term management of the extensive mature *Eucalyptus* plantations on Mt. Sutro, Mt. Davidson, and Monterey cypress plantations in the Presidio.

Floristic Analysis. Most of the scientific names applied to the Bolander collections have since been modified based on either replacement of misapplied European moss names or changes in species concepts as well as generic placement. When the species circumscription differs from the name referenced by Brandegee (1891) Lesquereux (1868) or Watson (1880), we have provided the synonymy as

far as we can determine it for that specimen. We have attempted to locate all of the Bolander collections obtained from San Francisco. We also cite the herbaria and collectors where other San Francisco specimens are deposited. One feature of this specimen-based catalogue is to list for each taxon the earliest collection date found among herbarium records examined. The California Academy of Sciences began operation in 1853. We speculate, however, that some moss specimens from the Bolander era may also have been lost in the 1906 earthquake and fires that ravaged the City and damaged the California Academy of Sciences building which was at that time located on Market Street.

Distribution of mosses within the City and County of San Francisco is directly related to substrate preference and habitat availability (Table 1). The number of mosses occurring within the study area is, in our view, relatively species rich for such a highly urbanized area. We were, however, surprised by the number of common coastal species of the California bryoflora found in adjacent Marin and San Mateo counties that were not encountered during this study. We attribute these "missing taxa" to several factors. San Francisco seems to have lacked a native coast redwood forest similar to that found in the vicinity of Mt. Tamalpais in Marin County to the north or in the Santa Cruz Mountains region in Santa Cruz and San Mateo counties to the south. According to historic accounts trees were an uncommon feature of the San Francisco landscape (Howell, Raven & Rubtzoff 1958). This lack of native forests in San Francisco is most likely the result of the strong winds that regularly channel through the San Francisco Bay and the extensive sand dune system that covered the western portion of San Francisco. Whatever native forest stands did exist were restricted to the higher peaks and then probably heavily utilized for both lumber and fuel wood consumption during the early years of growth of both Mission Dolores and the Presidio of San Francisco.

Compared with other tree species along the coast, such as *Acer macrophyllum* Pursh, *Alnus rubra* Bong., *Quercus spp.,* and *Umbellularia californica* (Hook & Arn.) Nutt., the bark of both *Eucalyptus* and *Cupressus* appears to be limiting as a primary substrate supporting moss colonization. Where *Eucalyptus* dominates, its bark shedding characteristic coupled with a thick leaf litter can be quite an impediment to moss colonization that prefer soil or bark. Even where moss occurs on the trunks and bases of *Eucalyptus,* it is not widespread within a particular stand of trees. There appears to be a considerable amount of unoccupied habitat. The bark of *Cupressus macrocarpa* is well furrowed and thick, but we speculate that its density and composition does not readily permit moisture absorption. Even when wetted, the bark dries quickly. This would seem to explain why mosses are infrequently encountered on Monterey cypress

except at the very base, among buttresses, or exposed roots. Bark chemistry may also be a factor in limiting moss colonization on Monterey cypress. Aside from these factors, the cypress canopies are nearly impervious to all but the heaviest rain, and this coupled with a outwardly descending branch arrangement moves moisture away from the trunk. The area beneath cypress trees is therefore dry much of the year. Stands of horticultural pines dominated by Monterey pine (*Pinus radiata* D. Don), while covered in lichens, generally lack mosses altogether. Again we speculate that the bark is not a suitable substrate for moss colonization within the climatic parameters present in San Francisco.

Many wooded or forested areas are also choked with a dense understory of non-natives dominated by French broom (*Genista monspessulana* (L.) L. Johnson), English ivy (*Hedera helix* L., Cape ivy (*Delairea odorata* Lem.), nasturtium (*Tropaeolum majus* L.) and/or Himalayan blackberry (*Rubus discolor* Weihe & Nees). Only grasslands provide relatively open patches of gravelly or rocky soils where mosses have a chance to compete. Another major factor influencing moss colonization relates directly to the geological parent rock material. Franciscan chert, the most common rock type in San Francisco appears to be a poor substrate for the establishment of mosses due to its flaking and fracturing characteristics. Other rock types are rare to uncommon within the City and County and that limits the potential for establishment of species that prefer a different rock or soil chemistry. For example, granitic rocks are only present at the Farallon Islands and limestone is completely lacking. Only one rocky outcrop was found to contain enough lime to support a colony of *Gymnostomum aeruginosum,* an obligate calciphile. Besides rock and tree substrates that influence moss colonization, desiccation is also a factor due to the strong winds that frequently channel across the City from the Pacific Ocean.

Several cosmopolitan species are quite successful in the City and County and can be found on a wide assortment of substrates such as concrete retaining walls, bricks, sidewalks, and even asphalt. *Bryum, Didymodon, Grimmia, Syntrichia* and *Tortula* species are relatively common on such substrates. Besides the widespread taxa, a few species in San Francisco are clearly elements of other bryofloras that we view as representing recent introductions to California. Exactly when these taxa were introduced remains speculative, but a few have been around for several decades and can be considered naturalized in California. These introduced mosses include *Bryum pyriferum, Calliergonella cuspidata, Campylopus introflexus, Campylopus pyriformis, Campylopus subulatus, Heterocladium dimorphum, Sematophyllum adnatum, Vesicularia vesicularis* and *Zygodon menziesii.* Of these taxa, *Bryum pyriferum, Campylopus pyriformis, Heterocladium dimorphum, Sematophyllum adnatum* and *Zygodon*

TABLE 1.   GENERALIZED HABITAT PREFERENCES FOR MOSSES IN SAN FRANCISCO.

Soil and gravels

Atrichum undulatum
Barbula convoluta
Bryum argenteum
Bryum bicolor
Bryum canariense
Bryum capillare
Bryum gemmascens
Bryum gemmilucens
Bryum lisae
Bryum pseudotriquetrum
Bryum torquescens
Ceratodon purpureus
Claopodium whippleanum
Dicranella heteromalla
Dicranella howei
Dicranella varia
Didymodon insulanus
Didymodon umbrosus
Didymodon vinealis
Ditrichum ambiguum
Ditrichum schimperi
Epipterygium tozeri
Fissidens bryoides longifolius
Fissidens crispus
Fissidens curvatus
Fissidens minutulus
Fissidens sublimbatus
Funaria hygrometrica
Funaria muhlenbergii
Homalothecium arenarium
Kindbergia praelonga
Pohlia nutans
Polytrichastrum alpinum
Polytrichum juniperinum
Polytrichum piliferum
Pseudocrossidium obtusulum
Pseudotaxiphyllum elegans
Scleropodium californicum
Scleropodium cespitans
Scleropodium julaceum
Syntrichia amplexa
Syntrichia bolanderi
Timmiella anomala
Timmiella crassinervis
Tortula obtusifolia
Triquetrella californica
Weissia controversa

Ephemeral mosses on soil (observed primarily during winter months)

Acaulon rufescens
Chenia leptophylla
Entosthodon bolanderi
Ephemerum serratum
Fissidens bryoides longifolius
Fissidens crispus
Fissidens curvatus
Fissidens minutulus
Fissidens sublimbatus
Funaria muhlenbergii
Hennediella heimii
Hennediella stanfordensis
Microbryum starkeanum

TABLE 1.   CONTINUED.

Phascum cuspidatum
Pleuridium acuminatum
Pleuridium sublatum
Pseudocrossidium obtusulum

Rock outcrops

Anacolia menziensii
Bartramia stricta
Bryum canariense
Bryum capillare
Bryum pyriferum
Campylopus introflexus
Dicranella heteromalla
Dicranoweisia cirrata
Didymodon vinealis
Grimmia laevigata
Grimmia lisae
Grimmia montana
Grimmia pulvinata
Grimmia trichophylla
Homalothecium arenarium
Homalothecium nuttallii
Isothecium cristatum
Kindbergia praelonga
Plagiothecium laetum
Polytrichum juniperinum
Polytrichum piliferum
Porotrichum bigelovii
Pterogonium gracile
Scleropodium californicum
Syntrichia amplexa
Syntrichia princeps
Triquetrella californica

Leaf litter

Dicranum howellii
Eurhynchium hians
Homalothecium arenarium
Kindbergia oregana
Kindbergia praelonga

Tree trunks, branches or exposed roots

Alsia californica
Amblystegium serpens
Antitrichia californica
Bryolawtonia vancouveriensis
Bryum argenteum
Bryum canariense
Campylopous subulatus
Dicranoweisia cirrata
Dicranum fuscescens
Heterocladium dimorphum
Isothecium cristatum
Isothecium myosuroides
Isothecium spiculiferum
Orthotrichum consimile
Orthotrichum diaphanum
Orthotrichum lyellii
Orthotrichum tenellum
Pterogonium gracile
Syntrichia pagorum
Syntrichia princeps
Tortula papillosa
Tortula plinthobia
Zygodon menziesii
Zygodon rupestris

TABLE 1.   CONTINUED.

Rotten wood and logs

  Amblystegium serpens
  Aulacomnium androgynum
  Dicranoweisia cirrata
  Isothecium cristatum
  Isothecium myosuroides
  Isothecium spiculiferum
  Kindbergia oregana
  Kindbergia praelonga
  Orthodicranum tauricum
  Plagiothecium laetum
  Sematophyllum adnatum

Seeps and wet places

  Amblystegium juratzkanum
  Amblystegium serpens
  Brachythecium asperrimum
  Brachythecium rutabulum
  Brachythecium salebrosum
  Bryum capillare
  Crumia latifolia
  Didymodon tophaceus
  Drepanocladus aduncus
  Fontinalis neomexicana
  Gymnostomum aeruginosum
  Hygroamblystegium tenax
  Kindbergia oregana
  Kindbergia praelonga
  Leptobryum pyriforme
  Leptodictyum riparium
  Orthotrichum rivulare
  Pohlia wahlenbergii
  Porotrichum bigelovii
  Scleropodium cespitans
  Scleropodium colpophyllum
  Scleropodium julaceum
  Scleropodium obtusifolium
  Scleropodium touretii
  Vesicularia vesicularis

Lawns

  Amblystegium serpens
  Brachythecium asperrimum
  Brachythecium rutabulum
  Calliergonella cuspidata
  Campylopus pyriformis
  Kindbergia praelonga
  Leptodictyum riparium
  Rhytidiadelphus squarrosus
  Scleropodium californicum
  Scleropodium cespitans
  Scleropodium colpophyllum

Concrete walls, bricks, sidewalks, buildings, asphalt

  Bryum argenteum
  Bryum capillare
  Ceratodon purpureus
  Didymodon australasiae
  Didymodon nicholsonii
  Didymodon rigidulus
  Didymodon umbrosus
  Didymodon vinealis
  Funaria hygrometrica
  Grimmia pulvinata
  Homalothecium nuttallii
  Isothecium cristatum

TABLE 1.   CONTINUED.

  Orthotrichum diaphanum
  Orthotrichum tenellum
  Philonotis capillaris
  Syntrichia ruralis
  Syntrichia princeps
  Tortula atrovirens
  Tortula brevipes
  Tortula latifolia
  Tortula muralis
  Tortula obtusifolia
  Tortula papillosa

menziesii are new additions to the California bryoflora. *Zygodon menziesii,* native to Chile, Australia and New Zealand is reported here for the first time in North America. Considering the number of potential introduction sites from the horticultural trade and the diversity of cultivated plants imported from all over the world to San Francisco, it is somewhat remarkable that so few exotic mosses have actually become established and naturalized. It seems likely that both habitat and substrate availability coupled with climatic factors are indeed real barriers to moss establishment in San Francisco. Mosses not accustomed to a Mediterranean-type environment with growth primarily restricted to the cool wet winter season followed by an extended summer drought period are unlikely to become a naturalized component of the California bryoflora. The four highest peaks in the City also form a rain shadow effect that is quite evident during the summer fog periods. The *Eucalyptus* plantations on Mt. Sutro and Mt. Davidson during the summer months are commonly engulfed in fog while the eastern portion of the City remains relatively sunny and dry. The associated fog drip may account for the diversity of mosses encountered on these two peaks within the City and County of San Francisco.

tion in this catalogue. Finally, we thank Dan Norris who has been extremely helpful and supportive throughout this project. He provided determinations or confirmations for many specimens in this catalogue and he has inspired us to work on moss floristics.

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CATALOGUE OF MOSSES

Acaulon rufescens Jaeg. [= *Sphaerangium muticum* (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On exposed soil. Grounds and fields of meadows, Mission Dolores, *Bolander s.n.* (UC) [confirmed by Toren]. Although habitat for this species still remains in San Francisco, we did not encounter it during this study.

Alsia californica (Hook. & Arnott) Sull. First record: 1866. On branches and trunks of both hardwood and conifer trees, especially *Quercus, Pittosporum, Salix, Eucalyptus* and *Cupressus.* Mission Dolores, *Kellogg s.n.* (CAS); The Dell, Lone Mountain, *Kellogg s.n.* (CAS); San Francisco, *Bolander s.n.* (UC); Golden Gate Heights Park, *Toren 7942* (CAS) & *Shevock 19200* (CAS, UC); Glen Canyon, San Miguel Hills, *Shevock 18878 & 18880* (CAS, UC); Golden Gate Park: Botanical Garden, *Hermann 17445* (CAS), near middle lake of Chain of Lakes, *Shevock 19210* (CAS, UC), near Stow Lake, *Shevock 18761 &*

18765 (CAS, MO, UC); near Elk Glen Lake, *Shevock 18894* (CAS, MO, UC), Paperback Cross, *Shevock 18804* (CAS, UC); Panhandle, *Toren 7801* (CAS) and near Conservatory of Flowers, *Toren 7747* (CAS) & *Shevock 18802* (CAS, UC); Brotherhood Way near Lake Merced, *Shevock 19286* (CAS, UC); Mt. Sutro, *Shevock 19186* (CAS, UC); Lafayette Park, *Shevock 19249* (CAS, UC).

Amblystegium juratzkanum Schimp. First record: 1953. Golden Gate Park, Japanese Tea Garden, *V. S. Bryan 33* (herb. not stated) [specimen cited in Steere, Anderson & Bryan 1954].

Amblystegium serpens (Hedw.) Schimp. in B.S.G. First record: 1962. On lawns, base of tree trunks and occasionally concrete retaining walls. Golden Gate Heights Park, *Toren 7946* (CAS); El Polin Loop, Presidio of San Francisco, *Shevock 19230* (CAS, UC); Lafayette Park, *Shevock 19238, 19239 & 19248* (CAS, UC); Jefferson Square, *Shevock 18898* (CAS, UC); Alta Plaza, *Shevock 19255* (CAS, UC); Mission Dolores Park, *Shevock 18989 & 19991* (CAS, UC); Walton Park, *Shevock 19305* (CAS, UC); Embarcadero near Pier 29 & 31, *Shevock 19105* (CAS, MO, UC); Lone Mountain, University of San Francisco, *Shevock 19339* (CAS, UC); Golden Gate Park: *Koch 1635 & 2308* (UC), *Wagner s.n.* (UC), *Norris 97033* (UC); Strybing Botanical Garden, *Hermann 17444* (CAS) & *Shevock 19514* (CAS, UC), Conservatory of Flowers, *Shevock 19307 & 19308* (CAS, UC), Panhandle, *Toren 7800* (CAS), *Shevock 18764* (CAS, UC), *Shevock 18774* (CAS, MO, UC), *Shevock 18933* (CAS, UC), De Laveaga Dell, Aids Memorial Grove, *Shevock 19524* (CAS, UC); Golden Gate National Recreation Area: Fort Mason, *Shevock 19091* (CAS, UC) and Aquatic Park, *Shevock 19096* (CAS, UC); Third at Burke Streets, *Shevock 20204* (CAS, UC).

Anacolia menziesii (Turn.) Par. First record: 2000. On soil over rock. Open space (future park) at Castro and 30th Streets. *Toren 8020* (CAS).

Antitrichia californica Sull. in Lesq. First record: 2000. On concrete retaining wall. Generally found on tree trunks or boulders. Yerba Buena Island, *Shevock 19111* (CAS, UC); Alcatraz Island, Golden Gate National Recreation Area, *Shevock, Toren & Thomas 20210a* (CAS).

Atrichum undulatum (Hedw.) P. Beauv. [Lesquereux 1868]. First record: 1868. On exposed mineral soils. Mission Dolores, *Bolander s.n.* (not located at UC). Although habitat exists for this moss in the City especially on Mt. Davidson and Mt. Sutro, we did not encounter it during our study.

Aulacomnium androgynum (Hedw.) Schwaegr. First record: 2000. On rotten wood and logs. Golden Gate Park near Strawberry Hill, *Shevock 19161* (CAS, MO, UC) and Chain of Lakes, *Shevock 19207* (CAS, UC); Mt. Sutro, *Toren 7749* (CAS).

Barbula convoluta Hedw. [Lesquereux 1868]. First record: 1868. On exposed soil. In gardens, San Francisco, *Bolander s.n.* (UC); Stow Lake, Golden Gate Park, *Koch 2310* (UC); De Laveaga Dell, Aids Memorial Grove, *Shevock 19517* (CAS, UC); along California Academy of Sciences building, *Shevock 18752* (CAS, UC); Twin Peaks, *Eastwood 57* (MO) [det. by Zander] and *Eastwood 59* (CAS) [det. by Bartram]; Mt. Sutro, *Toren 7773* (CAS); Cesar Chavez Street at highway 101, *Toren 7816* (CAS); Below overpass of highway 101 near Pet Cemetery, Presidio of San Francisco, *Shevock 19365* (CAS, UC).

Barbula unguiculata Hedw. First record: 2000. On exposed soil. Grand View below Twin Peaks, *Toren 7743* (CAS); Golden Gate Park and 41st Avenue and Lincoln Way, *Toren 8023* (CAS); West Pacific Street near Arguello Gate, Presidio of San Francisco, *Shevock 19360* (CAS, UC).

Bartramia stricta Brid. [Lesquereux 1868]. First record: 1868. On over rock. On moist rocks and ground around San Francisco, *Bolander s.n.* (UC); Glen Canyon, San Miguel Hills, *Shevock 18884* (CAS, UC); O'Shaughnessy Blvd., Glen Canyon, *Toren 7812* (CAS).

Brachythecium asperrimum (C. Müll.) Sull. First record: 1975. On lawns and grassy areas. Mary Ward Hall, San Francisco State University, *Showers 2852* (SFSU) [confirmed by Toren]; Golden Gate Park near Chain of Lakes, *Shevock 19163* (CAS, UC); Mt Sutro, *Shevock 19185* (CAS, UC); Turk and Mason Streets, *J. T. Howell s.n.* (CAS).

Brachythecium rutabulum (Hedw.) Schimp. in B. S. G. First record: 2000. On lawns and grassy areas. Near Pet Cemetery below highway 101, Presidio of San Francisco, *Shevock 19367* (CAS, UC) [det. by Norris].

Brachythecium salebrosum (Web. & Mohr.) Schimp. in B. S. G. First record: 2000. On soil with seep or wet areas over rock. Cesar Chavez Blvd. At highway 101, *Shevock 19276* (CAS, UC) [det. by Norris].

Bryolawtonia vancouveriensis (Kindb. in Mac.) Norris & Enroth First record: 2000. On base of tree trunks or exposed roots. Golden Gate Heights Park, *Toren 7943* (CAS) & *Shevock 19202* (CAS, MO, NY, UC); Golden Gate Park, De Laveaga Dell, Aids Memorial Grove, *Shevock 19521* (CAS, UC).

Bryum argenteum Hedw. [Lesquereux 1868]. First record: 1862. On exposed disturbed soils, concrete walls or base of tree trunks. Between Mission Dolores and the sea, *Brewer 898* (CAS, UC); Common around San Francisco, *Bolander s.n.*(UC); near Sutrowood and Stanyan Street, *Eastwood 55* (CAS); near Lake Merced, *Koch 1633* (UC); Jefferson Square, *Shevock 18903* (CAS); Bay View Park west of Candlestick, *Toren 7834* (CAS); Aqua Vista Park, *Shevock 18994* (CAS, MO, UC); Balboa Park, *Shevock*

19280 (CAS, UC); Lafayette Park, *Shevock 19237* (CAS, MO, UC); Third and Burke Streets, *Shevock 20205* (CAS, UC).

Bryum bicolor Dicks. [= *Bryum californicum* (Brandegee 1891 & Lesquereux 1868), *B. occidentale* (Brandegee 1891) and = *Bryum dichotomum*]. First record: 1868. On soil. Common around San Francisco, on the ground in grassy places, *Bolander s.n.* (UC); sand dunes, *Olson-Seffer s.n.* (UC) [det. by Koch; confirmed by Toren]; Mt. Sutro, *Toren 7774* (CAS); Bay View Park west of Candlestick, *Toren 7832* (CAS); Alta Plaza, *Shevock 19256* (CAS, UC); Lafayette Park, *Shevock 19234* (CAS, UC).

Bryum canariense Brid. First record: 2000. On soil, occasionally on rock outcrops or base of tree trunks. Park Blvd., entrance of Fort Winfield Scott, Presidio of San Francisco, *Shevock 19369* (CAS, UC); Golden Gate National Recreation Area: Fort Miley, *Shevock 19372* (CAS, UC) & Fort Funston, *Shevock 19159* (CAS, UC); Cesar Chavez Blvd. At highway 101, *Shevock 19277* (CAS, UC); Twin Peaks, *Shevock 18864* (CAS, UC); Southeast Farallon Island, Farallon National Wildlife Refuge, *Shevock 20147 & 20151* (CAS, UC); Corona Heights, *Shevock 18821* (CAS, UC); Bay View Park, *Shevock 19020* (CAS, UC); Twin Peaks, *Shevock 18869* (CAS, UC); Yerba Buena Island, *Shevock 19117* (CAS, MO, UC); Alamo Square, *Shevock 18906* (CAS, UC).

Bryum capillare Hedw. First record: 1868. On soil, rock outcrops or concrete retaining walls. Sandy soils near coast, *Bolander s.n.* (UC); Golden Gate Park, *Wagner 2363* (UC) [det. by Koch; confirmed by Toren]; Alamo Square, *Shevock 18913* (CAS, UC); Paramount Terrace off Stanyan Street, *Toren 7752* (CAS); Douglass Playground, *Toren 7782* (CAS); between Marietta Drive and O'Shaughnessy Blvd., *Toren 7807* (CAS); Bay View Park west of Candlestick, *Toren 7829a* (CAS) & *Shevock 19014* (CAS, UC); Potrero Hill, *Toren 7825* (CAS); Brotherhood Way near Lake Merced Blvd., *Toren 7946b* (CAS); Glen Canyon, San Miguel Hills, *Shevock 18889* (CAS, UC); Bernal Heights Park, *Shevock 19126* (CAS, UC); 14th Avenue and Ortega Street, *Shevock 19144* (CAS, UC); Stern Grove and Pine Lake Park, *Shevock 19158* (CAS, MO, UC); Mt. Sutro, *Shevock 19172* (CAS, UC); Alta Plaza, *Shevock 19259* (CAS, UC); Golden Gate Heights Park, *Shevock 19196* (CAS, UC); Presidio of San Francisco: Fort Point, *Shevock 18941* (CAS, UC) and near Pet Cemetery below highway 101, *Shevock 19222* (CAS, UC); Alcatraz Island, Golden Gate National Recreation Area, *Shevock, Toren & Thomas 20210* (CAS, UC).

Bryum gemmascens Kindb. First record: 2000. On soil, rock and gravels. Bernal Heights Park, *Toren 7792* (CAS); Cesar Chavez Blvd. at highway

101, *Toren 7818* (CAS); Castro and 30th Streets, *Toren 8017* (CAS); Glen Canyon Park, San Miguel Hills, *Shevock 18887* (CAS, UC); Aqua Vista Park, *Shevock 18995* (CAS, UC); Fort Point, Presidio of San Francisco, *Shevock 18937* (CAS, UC).

Bryum gemmilucens Wilcz. & Dem. First record: 2000. On soil and gravels. Aqua Vista Park, *Shevock 18993* (CAS, UC) [det. by Norris].

Bryum lisae De Not. First record: 2000. On rocky soils, retaining walls and bricks. Turk and Fillmore Streets, *Shevock 19343* (CAS, UC); Stern Grove and Pine Lake Park, *Shevock 19153* (CAS, UC); Twin Peaks, *Shevock 18870* (CAS, UC); Bay View Park, *Shevock 19011* (CAS, UC); Pacific Street, Presidio of San Francisco, *Shevock 19353* (CAS, UC); Golden Gate National Recreation Area: China Beach, *Shevock 19274* (CAS, UC) and between Painted Rock Cliffs and Sutro Park, *Shevock 18807* (CAS, UC).

Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer & Scherb. First record: 2000. On soil. Golden Gate Park between Middle and South Lake of Chain of Lakes west of the Polo Field, *Shevock 19206* (CAS, UC).

Bryum pyriferum Crundw. & H. Whiteh. First record: 2000. On rock wall. Alcatraz Island, Golden Gate National Recreation Area, *Toren, Shevock & Thomas 8459* (CAS) [det. confirmed by John Spence]. This collection represents the first documented occurrence of this species for California.

Bryum torquescens Bruch First record: 1947. On soil. Golden Gate Park, *Koch s.n.* (MICH) [cited by Syed 1973]; Lone Mountain, University of San Francisco, *Shevock 19334* (CAS, UC) [det. by Norris].

Calliergonella cuspidata (Hedw.) Loeske First record: 1969. In lawns and grassy areas. Fort Mason, Golden Gate National Recreation Area, *J. T. Howell s.n.* (CAS); A lawn weed at San Francisco State University, *Showers 450* (SFSU, UC); Mt. Sutro, *Toren 7771* (CAS); McLaren Park, *Shevock 19136* (CAS, MO, UC); Potrero del Sol Park, *Shevock 19278* (CAS, UC); Walton Park, *Shevock 19304* (CAS, UC).

Campylopus introflexus (Hedw.) Brid. First record: 2000. On rock outcrops with soil. Mt. Davidson, *Toren 7760* (BONN, CAS) [det by J-P. Frahm].

Campylopus pyriformis (F. Schultz) Bridel First record: 2000. On soil of lawn. Embarcadero at Chestnut Street across from Pier 29 & 31, *Shevock 19102* (BONN, CAS, MO, NY, UC) [det. by J-P. Frahm]. This collection represents the first documented occurrence of this species for California.

Campylopus subulatus Schimp. in Rabenh. First record: 2000. Base of tree trunks and on clayey soils. Panhandle, Golden Gate Park, *Shevock 18769* (BONN, CAS, MO, UC) & *18772* (BONN, CAS, NY, UC); Mt. Davidson, *Shevock 19291* (BONN, CAS, MO, UC) [dets. by J-P Frahm].

Ceratodon purpureus (Hedw.) Brid. First record: 1868. On soils and gravels, rock outcrops and occasionally at base of tree trunks. Mission Dolores, *Bolander s.n.* (UC); Sutrowood and Stanyan Street, *Eastwood 57* (CAS); Tank Hill, *Shevock 18919* (CAS, MO, UC); Twin Peaks, *Shevock 18862 & 19142* (CAS, UC), *Toren 7745* (CAS) and *Raven 21* (CAS); between Marietta Drive and O'Shaughnessy Blvd., *Toren 7813* (CAS); Bay View Park, *Shevock 19009* (CAS, MO, UC); Mt. Davidson, *Shevock 19289* (CAS, UC); Mt. Sutro, *Shevock 19194* (CAS, UC) & *19183* (CAS, UC); 14th Avenue at Ortega Street, *Shevock 19148* (CAS, UC); Golden Gate Heights Park, *Shevock 19203* (CAS, UC); Corona Heights Park, *Shevock 18824* (CAS, UC); Embarcadero near Piers 29 & 31, *Shevock 19104* (CAS, UC); McLaren Park, *Shevock 19135* (CAS, MO, UC); Coastal Bluff Trail, Golden Gate National Recreation Area, *Shevock 18805* (CAS, UC) & *18810* (CAS, MO, UC); Walton Park, Financial District, *Shevock 19301* (CAS, UC); Stanyan & Fulton Streets, Golden Gate Park, *Shevock 18837* (CAS, UC); Cesar Chavez Blvd. At highway 101, *Toren 7821* (CAS).

Chenia leptophylla (C. Müll.) Zand. First record: 1977. On exposed soils. Golden Gate Park near 41st Avenue and Lincoln Blvd., *Toren 2921* (CAS, SFSU).

Claopodium whippleanum (Sull. in Whipple & Ives) Ren. & Card. First record: 2000. On exposed soils and rock underhangs. Mt. Sutro, *Shevock 19167* (CAS, MO, UC) & *Shevock 19179a* (CAS, UC); Mt. Davidson, *Shevock 19289* (CAS, MO, UC) & *19297* (CAS, UC).

Crumia latifolia (Kindb. in Mac.) Schof. First record: 2000. On calcareous seeps. Coastal Bluff Trail, Golden Gate National Recreation Area, *Shevock 18815* (CAS, UC); Sutro Bath Site, Golden Gate National Recreation Area, *Shevock 19214* (CAS, UC).

Dicranella heteromalla (Hedw.) Schimp. First record: 2000. On clayey soils and crevices of rock outcrops. Mt. Davidson, *Shevock 18928* (CAS, MO, UC), *Shevock 19288* (CAS, UC), *19292* (CAS, MO, UC) and *Toren 7765* (CAS); Mt. Sutro, *Shevock 19171* (CAS, UC); Yerba Buena Island, *Toren 8054* (CAS); Fort Point, Presidio of San Francisco, *Shevock 18936* (CAS, UC); Southeast Farallon Island, Farallon National Wildlife Refuge, *Shevock 20148* (CAS, UC).

Dicranella howei Ren. & Card. First record: 1868. On clayey soils. Bay of San Francisco, *Bolander s.n.* (UC) [det. by Toren]; Coastal Bluff Trail, Golden Gate National Recreation Area, *Shevock 18806* (CAS, MO, UC); McLaren Park, *Shevock 19138* (CAS, UC).

Dicranella varia (Hedw.) Schimp. First record:

2000. On clayey soils. Bay View Park west of Candlestick, *Toren 7839* (CAS).

Dicranoweisia cirrata (Hedw.) Lindb. ex Milde First record: 1954. On tree trunks, exposed roots and rock outcrops. Mt. Davidson, *Toren 7770* (CAS); Golden Gate Heights Park, *Toren 7941* (CAS); 14th Avenue and Ortega Street, *Shevock 19149* (CAS, UC); Lincoln Park, Golden Gate National Recreation Area, *Shevock 19268* (CAS, MO, UC); Mt. Sutro, *Shevock 19180* (CAS, UC); Presidio of San Francisco, *Shevock 19355* (CAS, UC); Panhandle section of Golden Gate Park, *Shevock 20287* (CAS, UC) and horseshoe court near Stanyan and Fulton Sts., *Raven s.n.* (CAS) [det. by MacFadden; confirmed by Toren].

Dicranum fuscescens Turn. First record: 2000. On tree trunks. Mt. Sutro, *Shevock 19192* (CAS, UC).

Dicranum howellii Ren. & Card. First record: 2000. On soil and leaf litter. Mt. Davidson, *Shevock 19290* (CAS, MO, NY, UC) and *Toren 7767* (CAS).

Didymodon australasiae (Grev. & Hook.) Zand. First record: 2000. On concrete wall of buildings. Golden Gate Park, South Windmill, *Shevock 18896* (BUF, CAS, UC) [confirmed by Zander].

Didymodon insulanus (De Not.) M. Hill First record: 2000. On sandy soils. 14th Avenue and Ortega Street, *Shevock 19145* (CAS, UC) [det. by Norris].

Didymodon nicholsonii Culm. First record: 2000. On cement brick wall. Golden Gate Park at Willard North and Fulton Streets, *Shevock 18833* (CAS, UC) [det. by Norris].

Didymodon rigidulus Hedw. First record: 2000. On asphalt walkways. Golden Gate Park, De Laveaga Dell, Aids Memorial Grove, *Shevock 19515 & 20283* (CAS, UC).

Didymodon tophaceus (Brid.) Lisa [= *Trichostomum tophaceum* (Lesquereux 1868)]. First record: 1868. On wet soils and seeps generally with some salts. Fort Point (base of the Golden Gate Bridge), Presidio of San Francisco: *Bolander s.n.* (UC) & *Howe 55* (UC), *Shevock 18816 & 18934* (CAS, UC), *Toren 7742* (CAS), Baker Beach, *Shevock 18950 & 19152* (CAS, UC) and El Polin Spring, *Shevock 19231* (CAS, UC); Bay View Park west of Candlestick, *Toren 7841* (CAS) and *Shevock 19007* (CAS, MO, NY, UC); McLaren Park, *Shevock 19137* (CAS, UC); Lake Merced, *Raven 3* (CAS); Sutro Baths site, Golden Gate National Recreation Area, *Shevock 19211 & 19213* (CAS, UC), China Beach, *Shevock 19271 & 19272* (CAS, UC) and Lands End, *Eastwood s.n.* (CAS) [det. by Koch; confirmed by Toren]; Stow Lake, Golden Gate Park, *Shevock 18756* (CAS, UC).

Didymodon umbrosus (C. Müll.) Zand. First record: 2000. On compacted soils over concrete or asphalt. Aqua Vista Park, Central Basin, *Shevock*

18997 (BUF, CAS, MO, UC) [det. by Zander] & *Shevock 18992* (CAS, UC).

Didymodon vinealis (Brid.) Zand. [= *Barbula cylindrica, B. flexifolia, B. subfallax, B. vinealis & B. virescens* (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On soil, rock outcrops, concrete retaining walls and buildings. Presidio of San Francisco: Fort Point, *Bolander s.n.* (UC) & *Shevock 18938* (CAS, UC), Baker Beach, *Shevock 18951* (CAS), *Shevock 18946 & 18947* (CAS, UC), near Pet Cemetery below highway 101, *Shevock 19223* (CAS, UC) and Julius Kahn Playground near Locust Street, *Shevock 19351* (CAS, UC); Mission Dolores, *Howe 501* (CAS) and *Shevock 20282* (CAS, UC); Franklin and Pacific Streets, *Raven s.n.* (CAS); Turk & Fillmore Streets, *Shevock 19341* (CAS, UC); Mt. Davidson, *Shevock 19296* (CAS, UC); Mt. Sutro, *Shevock 19188* (CAS, UC); Buena Vista Park, *Shevock 18914* (CAS, MO, UC); Potrero Hill, *Toren 7826* (CAS), *Shevock 19001 & 19004* (CAS, UC); Twin Peaks, *Shevock 18865* (CAS, UC); Douglass Playground, *Toren 7781* (CAS); Bernal Heights Park, *Toren 7788* (CAS) and *Shevock 19127* (CAS, UC); Bay View Park west of Candlestick, *Toren 7838* (CAS); open space at 30th and Castro Street, *Shevock 19346* (CAS, UC); Yerba Buena Island, *Shevock 19115, 19118 & 20248* (CAS, UC); Kite Hill Park, *Shevock 19140* (CAS, UC); Stern Grove and Pine Lake Park, *Shevock 19150 & 19155* (CAS, UC); Golden Gate Heights Park, *Shevock 19197* (CAS, UC); Near Stanyan and Fulton Streets, *Raven s.n.* (CAS); Golden Gate Park: Lily Lake, *Shevock 18820* (CAS, UC); Mallard Lake, *Oberlander s.n.* (SFSU) [det. by Toren]; De Laveaga Dell, Aids Memorial Grove, *Shevock 19525* (CAS, UC), California Academy of Sciences building, *Shevock 18751* (CAS, UC); Golden Gate National Recreation Area: Fort Miley, USS San Francisco Memorial, *Shevock 19370* (CAS, UC); Lincoln Park, *Shevock 19265 & 19269* (CAS, UC), Fort Mason, Shevock 19093 (CAS, UC); Alcatraz Island, Golden Gate National Recreation Area, *Steen s.n.* (UC), *Toren 8469* (CAS) and *Shevock, Toren & Thomas 20211 & 20215* (CAS, UC).

Ditrichum ambiguum Best First record: 2000. On soil over rock. Mt. Davidson, *Toren 7805* (CAS).

Ditrichum schimperi (Lesq.) Kuntze First record: 2000. On soil over rock. Mt. Sutro, *Toren 7748* (CAS); Corona Heights, *Shevock 18882* (CAS, UC); Mt. Davidson, *Shevock 18926 & 19299* (CAS, UC); Glen Canyon, San Miguel Hills, *Shevock 18890* (CAS, MO, UC); Corona Heights, *Shevock 18822* (CAS, MO, UC); Yerba Buena Island, *Toren 8057* (CAS).

Drepanocladus aduncus (Hedw.) Warnst. [= *Hypnum aduncum* (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On wet lawns and saturated soils. Swamps near San Francisco, *Bolan-*

der s.n. (UC); Stonestown off of 19th Avenue, *Toren 8061* (CAS); Diamond Heights, 28th and Douglass Streets, *Toren 8458* (CAS).

Entosthodon bolanderi Lesq. [Lesquereux (1868)] First record: 1868. On soil. Clayey soil banks of the bay of San Francisco, *Bolander s.n.* (UC). Although habitat for this species still remains in San Francisco, we did not encounter this ephemeral species during our study.

Ephemerum serratum (Hedw.) Hampe [Lesquereux (1868)]. First record: 1868. On exposed soil. On the grounds and fields of meadows, Mission Dolores, *Bolander s.n.* (DUKE, UC) [confirmed by Toren]. Although habitat for this species still remains in San Francisco, we did not encounter this ephemeral species during our study.

Epipterygium tozeri (Grev.) Lindb. [= *Webera tozeri* (Brandegee 1891); *Bryum tozeri* (Lesquereux 1868)]. First record: 1868. On shaded clayey soils and rock underhangs. Borders of roads and ditches, San Francisco, *Bolander s.n.* (UC)*;* Corona Heights, *Shevock 18831* (CAS, MO, UC); Golden Gate Park, *Shevock 18836* (CAS, MO, UC); between Marietta Drive and O'Shaughnessy Blvd., *Toren 7811* (CAS); Douglass Playground, *Toren 7757* (CAS); Yerba Buena Island, *Shevock 19124* (CAS, MO, UC); Bernal Heights Park, *Shevock 19131* (CAS, UC); Fort Mason, Golden Gate National Recreation Area, *Shevock 19094* (CAS, MO, UC); Arguello at Washington Blvd., Presidio of San Francisco, *Shevock 19228* (CAS, MO, UC); Mt. Davidson, *Shevock 19298* (CAS, UC); Mt. Sutro, *Shevock 19178* (CAS, MO, UC); Alcatraz Island, Golden Gate National Recreation Area, *Toren 8468* (CAS).

Eurhynchium hians (Hedw.) Sande Lac. First record: 2000. On damp soil with leaf litter. Lone Mountain, *Shevock 19337* (CAS, UC) [det. by Norris].

Fissidens bryoides Hedw. var. longifolius (Brid.) Hampe [= *F. bryoides* var. *viridulus* (Swartz) Brotherus]. First record: 1962. On shaded clayey soils. Golden Gate Park, De Laveaga Dell, Aids Memorial Grove, *Hermann 17449* (CAS) [det. by Pursell]

Fissidens crispus Mont. [= *Fissidens limbatus* Sull. (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On shaded clayey soils. Common around San Francisco, *Bolander s.n.* (UC) [det. confirmed by Pursell]*; Golden* Gate Park near Conservatory of Flowers, *Toren 7746* (CAS) and *Raven 13* (CAS) [confirmed by Pursell]; Presidio of San Francisco: Coastal Bluff Trail, *Shevock 18943* (CAS, PAC, UC) and Arguello Blvd. at Washington Blvd., *Shevock 19227* (CAS, PAC, UC) [dets. by Pursell]; Golden Gate National Recreation Area: Coastal Bluff Trail near Sutro Park, *Shevock 18814* (CAS, PAC, UC) and Lincoln Park near Palace of the Legion of Honor, *Shevock 19263* (CAS, PAC, UC) [dets. by Pur-

sell]; Glen Canyon, *Shevock 18873* (CAS, PAC, UC) [det. by Pursell]; Bay View Park, *Shevock 19018* (CAS, PAC, UC) [det. by Pursell]; Mt. Sutro, *Shevock 19173 & 19175* (CAS, PAC, UC) [det. by Pursell]; Stern Grove, *Shevock 19156* (CAS, PAC, UC) [det. by Pursell]; Mt. Davidson, *Toren 7761* (CAS); Lone Mountain, *Shevock 19332* (CAS, MO, PAC, UC) [det. by Pursell]; Castro at 30th Street, *Shevock 19349* (CAS, PAC, UC) [det. by Pursell].

Fissidens curvatus Horsch. [= *Fissidens milo-bakeri* Koch]. First record: 2000. On clayey soils. Coastal Bluff Trail, Golden Gate National Recreation Area, *Shevock 18809* (CAS, MO, PAC, UC) [confirmed by Pursell]; along O'Shaughnessy Blvd. adjacent to west edge of Glen Canyon, *Shevock 18886* (CAS, PAC, UC) [confirmed by Pursell]; Buena Vista Park, *Shevock 18915* (CAS, PAC, UC) [confirmed by Pursell]; Douglass Playground, *Toren 7758* (CAS); Mt. Sutro, *Toren 7772* (CAS); Bernal Heights Park, *Toren 7793* (CAS); Yerba Buena Island, *Shevock 19125* (CAS, PAC, UC) & *Toren 8052* (CAS)[confirmed by Pursell]; Corona Heights, *Shevock 18830* (CAS, PAC, UC) [det. by Pursell]; Twin Peaks, *Shevock 18863 & 18872* (CAS, PAC, UC) [confirmed by Pursell].

Fissidens cf. *minutulus* Sullivant First record: 2000. Golden Gate Park, De Laveaga Dell, Aids Memorial Grove, *Shevock 20284* (CAS, PAC, UC) [det. by Pursell]

Fissidens sublimbatus Grout First record: 2000. On shaded clayey soils. Coastal Bluff Trail, Presidio of San Francisco, *Shevock 18945* (CAS, PAC, UC); Bay View Park, *Toren 7831* (CAS); Potrero Hill, *Toren 7824* (CAS) [dets. by Pursell]; Yerba Buena Island, *Shevock 20251* (CAS, PAC, UC) [det. by Pursell].

Fontinalis neomexicana Sull. & Lesq. First record: 1875. Attached to rocks in creek. *Vasey s.n.* (US) [cited by Welch 1960]. This species is likely extirpated from San Francisco due to lack of suitable habitat.

Funaria hygrometrica Hedw. First record: 1949. On moist or dry soils, retaining walls and other disturbed areas. Common on disturbed soils throughout the City. Golden Gate Park: California Academy Building, *Shevock 18753* (CAS, UC), Quarry Lake, *Raven 7* (CAS); Civic Center, *J. T. Howell s.n.* (CAS); Fillmore at Vallejo Street, *Raven s.n.* (CAS); Webster at Fillmore Street, *Raven s.n.* (CAS); east end of *22nd* Avenue, *J. T. Howell s.n.* (CAS); above Lake Merced, *Raven 4* (CAS); Baker Beach, Golden Gate Recreation Area, *Raven s.n.* (CAS); Aqua Vista Park, *Shevock 18996* (CAS, UC); Bay View Park, *Shevock 19015* (CAS, UC); Corona Heights, *Shevock 18827* (CAS, UC); Yerba Buena Island, *Shevock 19123* (CAS, MO, UC); Embarcadero across from Pier 29 & 31, *Shevock 19103* (CAS, UC); Aqua Vista Park, *Shevock*

18996 (CAS, UC); Golden Gate Heights Park, *Shevock 19195* (CAS, UC); Lake Merced, *Shevock 19287* (CAS, UC); Sutro Bath site, *Shevock 19216* (CAS, UC) and Fort Funston, Golden Gate National Recreation Area, *Shevock 19160* (CAS, UC); Lone Mountain, *Shevock 19338* (CAS, UC); Corona Heights above the Castro, *Shevock 18829* (CAS, UC); Alcatraz Island, Golden Gate National Recreation Area, *Toren 8467* (CAS).

Funaria muhlenbergii Turn. [= *Funaria mediterranea* (Brandegee 1891); *Funaria calcarea* (Lesquereux 1868)]. First record: 1868. On soil. Mission Dolores, *Bolander s.n.* (UC). Although habitat for this species still remains in San Francisco, we did not encounter this ephemeral species during our study.

Grimmia laevigata (Brid.) Brid. First record: 2000. On boulders and rock outcrops. Entrance to Hall of Man, California Academy of Sciences, Golden Gate Park, *Toren 7822* (CAS).

Grimmia lisae De Not. First record: 2000. On boulders, rock outcrops and concrete retaining walls. Twin Peaks, *Toren 7753* (CAS); Yerba Buena Island, *Toren 8056* (CAS) & *Shevock 19109* (CAS, MA, UC) [det. by Muñoz].

Grimmia montana Bruch & Schimp. in B.S.G. [Brandegee (1891); Lesquereux (1868)]. First record: 1868. On boulders and rock outcrops. San Francisco, *Bolander s.n.* (UC). Although habitat exists for the species in San Francisco, we did not encounter it during our study.

Grimmia pulvinata (Hedw.) Sm. First record: 2000. On boulders, rock outcrops and concrete retaining walls. Alamo Square, *Shevock 18912* (CAS); Clipper Street near Douglass Playground, *Toren 7779* (CAS); Bay View Park west of Candlestick, *Toren 7833* (CAS); Yerba Buena Island, *Shevock 19113* (CAS, MA, UC) [det. by Muñoz].

Grimmia trichophylla Grev. [= *Grimmia californica* (Brandegee 1891 & Lesquereux 1868) & *G. watsoni* (Brandegee 1891)]. First record: 1868. On boulders, rock outcrops and concrete retaining walls. Common around San Francisco, *Bolander s.n.* (UC); Golden Gate Heights Park, *Toren 7940* (CAS); Twin Peaks, *Shevock 18871* (CAS, UC) and *Toren 7744* (CAS); Mt. Sutro, *Shevock 19174* (CAS, UC); Glen Canyon, San Miguel Hills, *Shevock 18883* (CAS, MO, UC); Mt. Davidson, *Toren 7769* (CAS); Yerba Buena Island, *Shevock 19116* (CAS, UC); open space (Future park), corner of Castro and 30th Streets, *Toren 8015* (CAS); 14th & Ortega Streets, *Shevock 19147* (CAS, MA, UC) [det. by Muñoz].

Gymnostomum aeruginosum Sm. [= *Gymnostomum calcareum* var. *perpusillum* (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On shaded, moist calcareous soil over rock. San Francisco, *Bolander s.n.* (UC); Cesar Chavez Street at highway 101, *Toren 7817* CAS).

Hennediella heimii (Hedw.) Zand. First record:

2000. On exposed soil. Letterman Complex, Presidio of San Francisco, *Shevock 20207* (CAS, UC).

Hennediella stanfordensis (Steere) Blockeel First record: 2000. On exposed soil. Potrero Hill, *Toren 7827* (CAS); Cesar Chavez Street at highway 101, *Toren 7815* (CAS); Golden Gate Park, *Toren s.n.* (CAS, SFSU); Wayland and University Streets near McLaren Park, *Toren 7743b* (CAS); Bernal Heights Park, *Toren 7784* (CAS); Aqua Vista Park, Central Basin, *Shevock 18999* (CAS, UC), McKinley Square, *Shevock 19275* (CAS, UC); southeast end of Lake Merced. *Shevock 20286* (CAS, UC).

Heterocladium dimorphum (Brid.) Schimp. in B. S. G. First record: 2000. On tree trunks. Lafayette Park, *Shevock 19242* (CAS, NY, UC) & *19245* (CAS, MO, UC); Balboa Park, *Shevock 19279* (CAS, UC) [dets. by Norris]. These collections represent the first documented occurrences of this species for California.

Homalothecium arenarium (Lesq.) Lawt. [= *Hypnum arenarium* (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On soil, leaf litter and rock outcrops. Covering the sand among bushes near the shore, *Bolander s.n.* (UC); Twin Peaks, *Shevock 18868* (CAS, UC) and *Toren 7755* (CAS); Bay View Park, *Shevock 19013* (CAS, MO, UC); Bernal Heights Park, *Toren 7791* (CAS) & *Shevock 19130* (CAS, MO, UC); open space (future park) at Castro and 30th Streets, *Toren 8018* (CAS); Douglass Playground, *Toren 7776* (CAS); Kite Hill Park, *Shevock 19141* (CAS, UC); Baker Beach, Presidio of San Francisco, *Shevock 18948* (CAS, MO, UC).

Homalothecium nuttallii (Wils.) Jaeg. First record: 2000. On bases of tree trunks, rock outcrops and concrete and brick-like retaining walls. Buena Vista Park, *Shevock 18916* (CAS, UC); Bernal Heights Park, *Toren 7786* (CAS); Paramount Terrace off Stanyan Street, *Toren 7751* (CAS); Golden Gate Park, Panhandle, *Toren 7802* (CAS) & *Shevock 18768* (CAS, MO, UC); Yerba Buena Island, *Toren 8058* (CAS) & *Shevock 19119* (CAS, MO, UC); Mt. Sutro, *Shevock 19182* (CAS, MO, UC); near Crissy Field, Presidio of San Francisco, *Shevock 19224* (CAS, MO, NY, UC); Julius Kahn Playground, Presidio of San Francisco, *Shevock 19350* (CAS, MO, UC); Aquatic Park, Golden Gate National Recreation Area, *Shevock 19097* (CAS, MO, NY, UC); Alta Plaza Park, *Shevock 19262* (CAS, UC); Bay View Park, *Shevock 19019* (CAS, MO, NY, UC).

Hygroamblystegium tenax (Hedw.) Jenn. [= *Hygroamblystegium irriguum* in Steere, Anderson & Bryan 1954] First record: 1953. Golden Gate Park, Japanese Tea Garden, *L.E. Anderson 32* (herb. not cited) [specimen cited in Steere, Anderson & Bryan 1954].

Isothecium cristatum (Hampe) Robins. [= *Hypnum brewerianum* (Brandegee 1891 & Lesquereux

1868)]. First record: 1868. On exposed roots, logs and base of tree trunks, gravelly soils and rock outcrops and concrete retaining walls. On metamorphic sandstone around San Francisco, *Bolander s.n.* (UC); Glen Canyon, San Miguel Hills, *Shevock 18875 & 18891* (CAS, MO, UC); Corona Heights, *Shevock 18825* (CAS, UC); Mt. Sutro, *Shevock 19177* (CAS, UC), *Shevock 19169* (CAS, MO, UC) & *19187* (CAS, UC); open space (future park) corner of Castro and 30th Streets, *Toren 8021* (CAS) & *Shevock 19345* (CAS, UC); North Lake of Chain of Lakes, Golden Gate Park, *Shevock 19205* (CAS, UC); Presidio of San Francisco: Pacific Street near playground, *Shevock 19354 & 19357* (CAS, UC) and Presidio Golf Course, *Shevock 19363* (CAS, UC); Yerba Buena Island, *Shevock 20246 & 20249* (CAS, UC); Mt. Davidson, *Shevock 19293* (CAS, UC); between Painted Rock Cliffs and Sutro Park, Golden Gate National Recreation Area, *Shevock 18811* (CAS, MO, UC) [dets. by Norris].

Isothecium myosuroides Brid. [= *Hypnum myosuroides* (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On tree trunks, logs and rock outcrops. In dry woods, San Francisco, *Bolander s.n.*(UC); Mt. Davidson, *Shevock 18924 & 18927* (CAS, MO, UC) and *Toren 7766* (CAS); Mt. Sutro, *Shevock 19170, 19176, 19190, & 19193* (CAS, UC); Golden Gate Heights Park, *Toren 7945* (CAS); Brotherhood Way near Lake Merced, *Shevock 19285* (CAS, MO, UC); southeast side of Lake Merced, *Shevock 20285* (CAS, UC); Golden Gate National Recreation Area: Lincoln Park, Palace of the Legion of Honor, *Shevock 19264* (CAS, UC) and Coastal Bluff Trail between Painted Rock Cliffs and Sutro Park, *Shevock 18812* (CAS, UC) and Alcatraz Island, *Shevock, Toren & Thomas 20209* (CAS, UC).

Isothecium spiculiferum (Mitt.) Ren. & Card. First record: 2000. On tree logs. Mt. Sutro, *Shevock 19181* (CAS, UC); Golden Gate Park, Chain of Lakes, *Shevock 19204* (CAS, UC) [dets. by Norris].

Kindbergia oregana (Sull.) Ochyra [= *Eurhynchium oreganum* (Sull.) Jaeg.] First record: 2000. On soil with leaf litter and logs. Mt. Davidson, *Shevock 18923* (CAS); Mt. Sutro, *Shevock 19184* (CAS, MO, UC); Fort Point, Presidio of San Francisco, *Shevock 18939* (CAS, MO, UC); Lone Mountain, *Shevock 19336* (CAS, MO, NY, UC); Glen Canyon, San Miguel Hills, *Shevock 18877* (CAS, UC); Yerba Buena Island, *Shevock 20247* (CAS, UC).

Kindbergia praelonga (Hedw.) Ochyra [= *Eurhynchium praelongum* (Hedw.) Schimp. in B.S.G.]. First record: 1923. On soil with leaf litter, lawns, rock outcrops and tree trunks. Mt. Davidson, *Shevock 18925* (CAS, MO, UC), *Shevock 19294* (CAS, MO, UC), *Shevock 19295* (CAS, UC) & *Oberlander s.n.* (SFSU); Lone Mountain, *Shev-*

ock 19333 (CAS, MO, UC); Brotherhood Way near Lake Merced Blvd., *Toren 4946d* (CAS); Walton Park, *Shevock 19302* (CAS, UC); Lafayette Park, *Shevock 19243* (CAS, UC); Alamo Square, *Shevock 18907* (CAS, UC); Alta Plaza, *Shevock 19253* (CAS, UC); Golden Gate Heights Park, *Shevock 19199* (CAS, UC); Corona Heights, *Shevock 18828* (CAS, UC); Stern Grove and Pine Lake Park, *Shevock 19154 & 19157* (CAS, UC); McLaren Park, *Shevock 19134* (CAS, UC); Mt. Sutro, *Shevock 19168* (CAS, UC); Burke at Third Street, *Shevock 19006* (CAS, UC); Golden Gate Park: *Koch 1636* (UC), *Wagner 2365* (UC), *Koch 1636* (UC); Lily Lake, *Shevock 18817* (CAS, UC) & *Shevock 18818* (CAS, MO, UC), Mallard Lake, *Shevock 18893* (CAS, MO, UC), between Stow Lake and DeYoung Museum, *Shevock 18759* (CAS, MO, UC), Quarry Lake, *Raven 8 & Hermann 17448* (CAS), Rhododendron Grove, *Shevock 18762* (CAS, UC), Redwood Grove, Fulton Street near 12th Avenue, *Raven s.n.* (CAS), Conservatory of Flowers, *Shevock 18819* (CAS, UC), Panhandle, *Shevock 18770* (CAS, UC); hill near Cole Street, *Eastwood 58* (CAS), De Laveaga Dell, Aids Memorial Grove, Golden Gate Park, *Shevock 19516, 19518, & 19523* (CAS, UC), California Academy of Sciences, *Shevock 18754* (CAS, UC), Middle Chain of Lakes, *Shevock 19208* (CAS, UC), Strawberry Hill, *Shevock 19162, 19164, & 19166* (CAS, UC); Presidio of San Francisco: near Crissy Field, *Shevock 19226* (CAS, UC) & Fort Point, *Shevock 18935* (CAS, MO, UC), near Arguello Gate, *Shevock 19359* (CAS, UC), Letterman Complex, *Shevock 19217, 19218, & 19220* (CAS, UC), Pacific Street near playground, *Shevock 19358* (CAS, UC); Golden Gate National Recreation Area: Fort Mason, *Shevock 19092* (CAS, UC), Lincoln Park, *Shevock 19266* (CAS, UC).

Leptobryum pyriforme (Hedw.) Brid. First record: 1867. On soil of seepy areas. The Dell, Lone Mountain, *Kellogg s.n.* (CAS); Ewing Terrace, *Toren 7783* (CAS); Bay View Park, *Shevock 19016* (CAS, UC); Presidio of San Francisco near Arguello Gate, *Shevock 19361* (CAS, MO, UC) and just west of Pet Cemetery, *Shevock 19225 & 19366* (CAS, MO, UC).

Leptodictyum riparium (Hedw.) Warnst. First record: 2000. On saturated soils and lawns. Alamo Square, *Shevock 18909* (CAS, MO, UC); Embarcadero near Pier 29 & 31, *Shevock 19107* (CAS, UC).

Microbryum starkeanum (Hedw.) Zand. [= *Pottia starkeanum* (Brandegee 1891) & as *Anacalypta starkeana* (Lesquereux 1868)] First record: 1868. On bare soil. Mission Dolores, *Bolander s.n.* (UC); Golden Gate Park near 41st Avenue and Lincoln Blvd., *Toren 8022* (CAS).

Orthodicranum tauricum (Sapehin) Smirnova First

record: 2000. On rotten logs. Mt. Sutro, *Shevock 19191* (CAS, UC).

Orthotrichum consimile Mitten First record: 2000. On *Pittosporum* and *Myoporum* tree trunks. Diamond Heights, Duncan Street and Cameo Way, *Toren 8160* (CAS); Panhandle, Golden Gate Park, *Shevock 18932* (CAS, UC) [det. by Norris].

Orthotrichum diaphanum Brid. First record: 2000. On tree trunks and concrete retaining walls. Golden Gate Park, Panhandle, *Toren 7795* (CAS) & *Shevock* 18931 (CAS, MO, UC); Balboa Park, *Shevock 19283* (CAS, UC); Lafayette Park, *Shevock 19240* (CAS, MO, UC).

Orthotrichum lyellii Hook. & Tayl. First record: 2000. On tree trunks and branches. Golden Gate Park, Panhandle, *Shevock 18838 & 18932a* (CAS, UC) and De Laveaga Dell, Aids Memorial Grove, *Shevock 19519* (CAS, UC); Mt. Sutro, *Shevock 19300* (CAS, UC); Alamo Square, *Shevock 18905* (CAS, UC); Glen Canyon, San Miguel Hills, *Shevock 18881* (CAS, UC); Lafayette Park, *Shevock 19242* (CAS, UC); Embarcadero near Piers 29 & 31, *Shevock 19106* (CAS, UC); Letterman Hospital Complex, Presidio of San Francisco, *Shevock 19219* (CAS, UC) [det. by Vitt]; Third Street between Burke and Custer Streets, *Shevock 19005 & 20203* (CAS, UC) [det. by Vitt].

Orthotrichum rivulare Turn. First record: 1868? On rocks along stream. San Francisco, *Bolander s.n.* no date (UC). Although this Bolander collection attributed to San Francisco was not referenced by Brandegee (1891), the specimen is nonetheless accurately identified [det. confirmed by Norris]. This species is most likely extirpated from San Francisco with the elimination of free-flowing streams with bedrock.

Orthotrichum tenellum Bruch ex Brid. First record: 2000. On tree trunks and rock outcrops and concrete retaining walls. Panhandle of Golden Gate Park, *Toren 7794* (CAS), *Shevock 18763 & Shevock 18930* (CAS, UC); Yerba Buena Island, *Toren 8051* (CAS); Lafayette Park, *Shevock 19242* (CAS, UC); Jefferson Square, *Shevock 18902* (CAS, UC); Pershing Square, Presidio of San Francisco, *Shevock 19368* (CAS, UC); Holly Park, *Shevock 19132* (CAS, UC); Third and Burke Streets, *Shevock 20202* (CAS, UC); Southeast Farallon Island, Farallon National Wildlife Refuge, *Shevock 20149* (CAS, UC).

Phascum cuspidatum Hedw. [Brandegee (1891) & Lesquereux (1868)] First record: 1868. On exposed soil. On the grounds and fields and meadows, Mission Dolores, *Bolander s.n.* (UC) [confirmed by Toren]; Potrero Hill, *Toren 7823* (CAS).

Philonotis capillaris Lindb. in Hartm. First record: 2000. On moist soil over rock. Tank Hill, *Shevock 18918* (CAS, UC); Clipper Street near Douglass Playground, *Toren 7780* (CAS); Bernal Heights Park, *Toren 7790* (CAS).

Plagiothecium laetum Schimp. in B.S.G. First record: 2000. On logs and on moist soil with rock. Near Stow Lake, Golden Gate Park, *Shevock 18760* (CAS, MO, UC) & *19165* (CAS, MO, NY, UC) and near Chain of Lakes, *Shevock 19161a* (CAS); Mt. Davidson, *Toren 7763* (CAS).

Pleuridium acuminatum [= *Pleuridium bolanderi* C. Muell ex Jaeg.]. First record: 1868. On exposed soil. Near San Francisco, *Bolander s.n.*(UC); Mt. Davidson, *Shevock 18921* (CAS); Marietta Drive, *Toren 7810* (CAS); on hill near Sutrowood and Stanyan Street, *Eastwood 54* (CAS); Wayland at University Street near McLaren Park, *Toren 7743c* (CAS); Bernal Heights Park, *Toren 7787* (CAS); open space (future park) at corner of Castro and 30th Streets, *Toren 8016* (CAS); Diamond Heights, *Toren 8457* (CAS).

Pleuridium subulatum (Hedw.) Rabenh. First record: 1904. On exposed soil. Glen Canyon, San Miguel Hills, *Shevock 18888* (CAS, UC); Arguello Blvd. At Washington Blvd., Presidio of San Francisco, *Shevock 19229* (CAS, UC); Golden Gate Park, *Gardner s.n.* (UC) [dets. by Norris].

Pohlia nutans (Hedw.) Lindb. First record: 2000. On moist soils with rock. Mt. Davidson, *Toren 7762* (CAS).

Pohlia wahlenbergii (Web. & Mohr.) Andrews [= *Bryum albicans* (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On moist soil. On rocks watered by springs, *Bolander s.n,.* (UC) [det. confirmed by Shaw]. This species is likely extirpated from San Francisco due to a lack of suitable habitat.

Polytrichastrum alpinum (Hedw.) G. L. Sm. First record: 2000. On soil with rock. Mt. Davidson, *Toren 7764* (CAS).

Polytrichum juniperinum Hedw. First record: 1950. On soil among rock outcrops. Glen Canyon, San Miguel Hills, *Shevock 18882 & 18892* (CAS, MO, UC); Mt. Davidson, *Shevock 18922* (CAS, UC), *Toren 7750* (CAS) and *Raven 18* (CAS); Twin Peaks, *Shevock 18867* (CAS, UC); between Marietta Drive and O'Shaughnessy Blvd., *Toren 7808* (CAS); Douglass Playground, *Toren 7777* (CAS); Bay View Park, *Shevock 19010* (CAS, MO, UC); open space (future park) at corner of Castro and 30th Streets, *Toren 8014* (CAS).

Polytrichum piliferum Hedw. First record: 2000. On soil among rock outcrops. San Miguel Hills between Marietta Drive and O'Shaughnessy Blvd., *Toren 7809* (CAS); Diamond Heights, Duncan and Newburg Streets, *Toren 8456* (CAS).

Porotrichum bigelovii (Sull.) Kindb. First record: 1962. On shaded moist soil and rocks. De Laveaga Dell, Aids Memorial Grove, Golden Gate Park, *F. J. Hermann 17451* (CAS) & *Shevock 19526* (CAS, MO, NY, UC).

Pseudocrossidium obtusulum (Lindb.) Crum & Anderson First record: 2000. On soil. Cesar Chavez

Street at highway 101, *Toren 7820* (CAS); Bay View Park, *Toren 7835* (CAS).

Pseudotaxiphyllum elegans (Brid.) Iwats. First record: 1973. On shaded clayey soil. Mt. Davidson, *Toren & Wong 840* (CAS, SFSU) & *Toren 7804* (CAS); Mt. Sutro, *Shevock 19179* (CAS).

Pterogonium gracile (Hedw.) Sm. [Lesquereux (1868)]. First record: 1868. On rock outcrops and tree trunks. On ground and rocks, *Bolander s.n.*(UC). Although habitat for this species remains in San Francisco we did not encounter it during this study.

Rhytidiadelphus squarrosus (Hewd.) Warnst. First record: 1976. On lawn. Japanese Tea Garden, Golden Gate Park, *Toren, Showers, & Smith 2811* (SFSU).

Scleropodium californicum (Lesq.) Kindb. [= *Hypnum californicum* (Lesquereux 1868)]. First record: 1868. On soil with leaf litter, rock outcrops and concrete retaining walls. Near the Bay of San Francisco, *Bolander s.n.*(UC); Golden Gate National Recreation Area, Coastal Bluff Trail between Painted Rock Cliffs and Sutro Park, *Shevock 18808* (CAS, MO, UC) & *Shevock 18813* (CAS, UC), Fort Miley area, *Shevock 19371* (CAS, UC) and Alcatraz Island, *Shevock, Toren & Thomas 20214* (CAS, UC); South Windmill, Golden Gate Park, *Shevock 18897* (CAS, MO, UC); Fort Point, Presidio of San Francisco, *Toren 7741* (CAS); Potrero Hill, *Toren 7828* (CAS); Twin Peaks, *Toren 7756* (CAS); Bernal Heights Park, *Toren 7785* (CAS); Bay View Park, *Toren 7830 & 7840* (CAS); Golden Gate Heights Park, *Toren 7944* (CAS); Lake Merced, *Toren, Showers & Halling 1460* (SFSU); Clarendon Heights, *Howe 523* (CAS); Potrero Hill Park, *Shevock 19000* (CAS, UC); open space (future park) at Castro and 30th Streets, *Toren 8019* (CAS); Yerba Buena Island, *Toren 8059* (CAS), *Shevock 19112* (CAS, MO, UC), *Shevock 19120, 20245, 20250 & 20252* (CAS, UC).

Scleropodium cespitans (C. Müll.) L. Koch First record: 2000. On clayey soil, base of tree trunks and exposed roots, rock outcrops and concrete retaining walls. Yerba Buena Island, *Toren 8053 & 8060* (CAS); Walton Park, *Shevock 19303* (CAS, UC); below Coit Tower, *Shevock 19108* (CAS, MO, UC); Corona Heights, *Shevock 18823 & 18826* (CAS, UC); Golden Gate Heights Park, *Shevock 19198* (CAS, UC); Lafayette Park, *Shevock 19244 & 19247* (CAS, UC); Holly Park, *Shevock 19133* (CAS, UC); Grand View Park, *Shevock 19143* (CAS, UC); Glen Canyon, San Miguel Hills, *Shevock 18885* (CAS, UC); Golden Gate Park: California Academy of Sciences building, *Shevock 18755* (CAS, MO, UC), Panhandle, *Shevock 18771* (CAS, UC); Southeast Farallon Island, Farallon National Wildlife Refuge, *Shevock 20150 & 20152* (CAS, UC); Presidio of San Francisco: Letterman Complex, *Shevock 19221* (CAS, UC), Fort Point,

Shevock 18942 (CAS, UC), Baker Beach, *Shevock 18949* (CAS, UC).

Scleropodium colpophyllum (Sull.) Grout. First record: 2000. On soil and leaf litter, base of tree trunks and exposed roots, and concrete and brick retaining walls. Brotherhood Way near Lake Merced Blvd., *Toren 7946a* (CAS); Mission Dolores Park, *Shevock 18990* (CAS, UC); Alamo Square, *Shevock 18908* (CAS, UC); Glen Canyon, *Shevock 18876* (CAS, MO, UC); Turk & Fillmore Streets, *Shevock 19342* (CAS, UC); Stern Grove & Pine Lake Park, *Shevock 19151 & 19152* (CAS, UC); Golden Gate Park: near Conservatory of Flowers, *Shevock 18803* (CAS, UC), Panhandle, *Shevock 18766* (CAS, UC), De Laveaga Dell, Aids Memorial Grove, *Shevock 19520* (CAS, UC) & between Stow Lake and DeYoung Museum, *Shevock 18758* (CAS, MO, UC); Aquatic Park, Golden Gate National Recreation Area, *Shevock 19101* (CAS, UC); Alcatraz Island, Golden Gate National Recreation Area, *Toren 8461 & 8470* (CAS).

Scleropodium julaceum Lawt. First record: 2000. On clay soils and rock outcrops. Along Park Presidio (highway 1) between Lake and Sacramento Streets, *Shevock 19232* (CAS, UC); Potrero Hill Park, 22nd Street between Arkansas and Missouri Streets, *Shevock 19003* (CAS, UC).

Scleropodium obtusifolium (Mitt.) Kindb. in Mac. & Kindb, First record: 2000. On moist clayey soils over rocks. Lincoln Park, Golden Gate National Recreation Area, *Shevock 19267* (CAS, UC); Red Rock Hill, southeast corner of Duncan St. and Diamond Heights Blvd., *Toren 8504* (CAS).

Scleropodium touretii (Brid.) L. Koch [= *Hypnum illecebrum* (Brandegee 1891)]. First record: 1868. On clayey soil over rocks. Shady sandy ground, San Francisco, *Bolander s.n.* (UC)*;* Glen Canyon, San Miguel Hills, *Shevock 18874* (CAS, MO, UC); open space (future park) at Castro and 30th Streets, *Toren 8012* (CAS); Golden Gate Park, *Oberlander s.n.* (SFSU) [det. by Toren]; Twin Peaks, *Shevock 18866* (CAS, UC); Bernal Heights Park, *Shevock 19128* (CAS, UC); Yerba Buena Island, *Shevock 19121* (CAS, UC); Bay View Park, *Shevock 19012* (CAS, UC); Lone Mountain, University of San Francisco, *Shevock 19337* (CAS, UC)..

Sematophyllum adnatum (Michaux) Britton First record: 2000. On rotten logs. Mt. Davidson, *Shevock 18929* (CAS, MO, NY, UC) [det. confirmed by Norris]. This collection represents the first documented occurrence of this species for California.

Syntrichia amplexa (Lesq.) Zand. [= *Barbula amplexa* (Brandegee 1891)]. First record: 1868. On clayey soil and rocks. Near the Bay of San Francisco, *Bolander s.n.*(UC) and *Blasdale s.n.* (UC); Bay View Park, *Toren 7836* (CAS); China

Beach, Golden Gate National Recreation Area, *Shevock 19270* (CAS, UC).

Syntrichia bolanderi (Lesq. & James) Zand. [= *Barbula bolanderi* (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On soil. In gardens, San Francisco, *Bolander s.n.*(UC). Although habitat for this species still remains in San Francisco, we did not encounter it during this study.

Syntrichia pagorum (Milde) Amann First record: 2000. On tree trunks. Panhandle section, Golden Gate Park, *Toren 7799* (CAS); Lafayette Park, *Shevock 19246a* (CAS); Alamo Square, *Shevock 18910* (CAS, UC).

Syntrichia princeps (De Not.) Mitt. First record: 1868. On tree trunks, soil over rocks and concrete retaining walls. Mission Dolores, *Bolander s.n.* (UC) [det. by Norris]; Buena Vista Park, *Shevock 18917* (CAS, UC); Twin Peaks, *Toren 7754* (CAS); Yerba Buena Island, *Toren 8055* (CAS), *Shevock 19110 & 19114* (CAS, MO, UC); Pacific Street, Presidio of San Francisco, *Shevock 19352 &* 19356 (CAS, UC); Panhandle, Golden Gate Park, *Shevock 18767* (CAS, MO, UC); Alta Plaza, *Shevock 19260* (CAS, UC); Balboa Park, *Shevock 19284* (CAS, UC); Lafayette Park, *Shevock 19233* (CAS, UC); Bay View Park, *Shevock 19008* (CAS, UC); Alcatraz Island, Golden Gate National Recreation Area, *Shevock, Toren & Thomas 20213 & 20216* (CAS, UC).

Syntrichia ruralis (Hedw.) Web. & Mohr First record: 1868? On concrete retaining wall. Sand Hills, *E. L. Greene s.n.* (UC); Alta Plaza Park, *Shevock 19258* (CAS, UC) [dets. by Norris].

Timmiella anomala (Bruch & Schimp. in B. S. G.) Limpr. [= *Trichostomum anomalum* (Brandegee 1891)]. First record: 1868. On soil with rock. Near San Francisco, *Bolander s.n.*(UC); Bernal Heights Park, *Shevock 19258* (CAS, MO, UC) [det. by Norris].

Timmiella crassinervis (Hampe) L. Koch [= *Trichostomum flexipes* (Brandegee 1891)]. First record: 1868. On soil with rock. Common on shaded ground and decaying trunks, *Bolander s.n.* (UC); Wayland Street at University Street near McLaren Park, *Toren 7743a* (CAS); Mt. Sutro, *Toren 7775* (CAS); Bernal Heights Park, *Toren 7789* (CAS); Bay View Park, *Toren 7837* (CAS); Yerba Buena Island, *Shevock 19122* (CAS, UC); McLaren Park, *Shevock 19139* (CAS, UC).

Tortula atrovirens (Sm.) Lindb. [= *Desmatodon nervosus* var. *edentulus* (Brandegee 1891) & *Desmatodon californicus* (Lesquereux 1868)]. First record: 1868. On wall of buildings. Decaying ground of old walls of clay (adobe), San Francisco, *Bolander s.n.* (UC). Although habitat for this species still remains in San Francisco, we did not encounter it during this study.

Tortula brevipes (Lesq.) Broth. [= *Barbula brevipes* (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On buildings. Mud walls, Mission Dolores, in mats an inch broad or more, *Bolander s.n.* (UC). Although habitat for this species still remains in San Francisco, we did not encounter it during this study.

Tortula latifolia Bruch ex Hartm. First record: 2000. On concrete retaining walls. Yerba Buena Island, *Toren 8050* (CAS); Lafayette Park, *Shevock 19236* (CAS, MO, UC) [det. by Norris].

Tortula muralis Hedw. First record: 1923. On soil, base of tree trunk, boulders, rock outcrops, concrete retaining walls and buildings. San Francisco, *Sudiffe 49* (CAS); Francisco and Hyde Streets, *L. S. Rose s.n.* (CAS); University of San Francisco, Fulton at Parker Street, *Raven s.n.* (CAS); Balboa Street near Arguello, *Raven s.n.* (CAS); Filbert and Van Ness Avenue, *J. T. Howell s.n.* (CAS); 26th Avenue near El Camino del Mar, *Raven s.n.* (CAS); between Fillmore and Laguna Street, *Raven s.n.* (CAS); Alamo Square, *Shevock 18913* (CAS, UC); Yerba Buena Island, *Shevock 19118a & 20244* (CAS, UC); Potrero Hill Park, *Shevock 19002* (CAS, UC); Jefferson Square, *Shevock 18899 & 18904* (CAS, UC); Golden Gate Park: South Windmill, *Shevock 18895* (CAS, MO, UC), Fulton near 1st Avenue, *J. T. Howell s.n.* (CAS), Stanyon Street between Fulton & Hayes Streets, *Shevock 18834 & 18835* (CAS, UC), Quarry Lake, *Raven 5* (CAS), Stow Lake, *Shevock 18757* (CAS, UC) and De Laveaga Dell, Aids Memorial Grove, *Shevock 19522* (CAS, UC); Cesar Chavez Street at highway 101, *Toren 7814* (CAS); Lookout Point, *Halling 600* (SFSU) [confirmed by Toren]; Glen Canyon, San Miguel Hills, *Shevock 18879* (CAS, UC); Turk & Fillmore Streets, *Shevock 19340* (CAS, UC); Aqua Vista Park, *Shevock 18998* (CAS, UC); Alta Plaza Park, *Shevock 19261* (CAS, UC); Lafayette Park, *Shevock 19235* (CAS, UC); Presidio of San Francisco: Coastal Bluff Trail near Golden Gate Bridge, *Shevock 18940* (CAS, UC) and near Arguello Gate, *Shevock 19362* (CAS, UC);.Golden Gate National Recreation Area: Sutro bath site, *Shevock 19215* (CAS, UC) and Aquatic Park, *Shevock 19099* (CAS, UC).

Tortula obtusifolia (Schwaegr.) Math. [as *Desmatodon flavicans,* not in Brandegee 1891]. First record: 1868. On soil? Mission Dolores, *Bolander s.n.* (UC) [det. confirmed by Toren]. Although habitat for this species remains in San Francisco we did not encounter it during this study.

Tortula papillosa Wils. in Spruce First record: 2000. On tree trunks and concrete retaining wall. Twin Peaks, *Toren 7245* (CAS); Alta Plaza Park, *Shevock 19254 & 19257* (CAS, UC); Balboa Park, *Shevock 19281* (CAS, UC) & *Shevock 19282* (CAS, MO, UC); Jefferson Square, *Shevock 18900* (CAS, MO, UC); Lafayette Park, *Shevock 19251* (CAS, MO, UC); Presidio Golf Course, Presidio of San Francisco, *Shevock*

19364 (CAS, UC); Third Street at Burke Street, *Shevock 20201* (CAS, UC).

Tortula plinthobia (Sull. & Lesq.) Broth. First record: 2000. On bark of poplars. Third Street at Burke and Custer Streets, *Shevock 20206* (CAS, UC).

Triquetrella californica (Lesq.) Grout First record: 2000. On soils and rock outcrops. Tank Hill, *Shevock 18920* (BUF, CAS, UC)[confirmed by Zander]; Clipper Street at Douglass Playground, *Toren 7778* (CAS); open space (future park) at Castro and 30th Streets, *Toren 8013* (CAS); Diamond Heights, Duncan and Newburg Streets, *Toren 8455* (CAS).

Vesicularia vesicularis (Schwaegr.) Broth. First record: 1923. Wet areas of lawn. Golden Gate Park, *Bradshaw s.n.*(CAS), *Wagner s.n.*(CAS) and the Conservatory, *Toren 688* (CAS, SFSU).

Weissia controversa Hedw. [= *Weissia viridula* (Brandegee 1891 & Lesquereux 1868)]. First record: 1868. On soil. At and around San Francisco, *Bolander s.n.*(UC)*;* Mt. Davidson, *Toren 7768* (CAS); Brotherhood Way near Lake Mer-

ced Blvd., *Toren 7946c* (CAS); Aquatic Park, Golden Gate National Recreation Area, *Shevock 19095* (CAS, UC); open space at 30th & Castro St., *Shevock 19348* (CAS, UC).

Zygodon menziesii (Schwaegr.) Arnott First record: 2000. On trunks of *Eucalyptus* and *Myoporum.* Panhandle section of Golden Gate Park, *Toren 7797* (CAS) and *Shevock 18773* (ALTA, CAS, MO, UC); Jefferson Park, *Shevock 18901* (ALTA, CAS, NY, UC) [dets.confirmed by Vitt]; Diamond Heights, Duncan Street and Cameo Way, *Toren 8159* (CAS). These collections represent the first documented occurrences of this species for California and North America.

Zygodon rupestris (Lindb. ex Hartm.) Lindb. ex Britt. First record: 1976. On trunks of *Eucalyptus* and *Cupressus.* St. Francis Blvd., *Toren 5001* (CAS); Mt. Davidson, *Toren 7759* (CAS); Golden Gate Park, Panhandle, *Toren 7796* (CAS); Golden Gate Heights Park, *Toren 7939* (CAS) & *Shevock 19201* (ALTA, CAS, MO, UC); Lafayette Park, *Shevock 19246* (CAS, NY, UC) & *19250* (ALTA, CAS, MO, UC).

BRYOPHYTE FLORA OF WILLIAM L. FINLEY NATIONAL WILDLIFE REFUGE, WILLAMETTE VALLEY, OREGON

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ABSTRACT

The Willamette Valley in northwestern Oregon is a mosaic of plant communities, some of which have become rare following European settlement. William L. Finley National Wildlife Refuge preserves examples of many of these historic communities, which provide diverse substrates for bryophytes. Mosses and liverworts were collected at the refuge from 1993 through 1999. Eighty-four moss and 24 liverwort species were identified and their substrates cataloged. The moss *Physcomitrella patens* (Hedwig) Bruch, Schimper & Gümbel is newly reported for Oregon. The rarity of some common Pacific Northwest species at Finley Refuge may be a function of the drier climate in the Willamette Valley than in the surrounding mountain ranges. Land at Finley Refuge is managed primarily for wildlife species, but the protection of natural and pre-settlement plant communities has resulted in conditions facilitating a rich bryophyte flora.

The Willamette Valley in northwestern Oregon provides a diversity of bryophyte substrates that differ from those in the surrounding mountain forests because of its contrasting climate and vegetation. The presence of hardwoods as well as conifers, open as well as closed canopies, wetlands as well as uplands, and human-altered as well as natural landscapes provide a plethora of substrates supporting a rich bryoflora. Willamette Valley bryophytes have been variously surveyed (Sanborn 1929; Chapman and Sanborn 1941; Pike 1973; Pike et al. 1975), but no intensive collections of all substrates within a defined geographic area have been made. This study of a representative Willamette Valley location appears to be the first inventory of all substrates within such a defined area.

Warmer and drier than the surrounding mountains, the Willamette Valley is a broad depression between the Coast and Cascade Ranges, extending from the Columbia River south to the convergence of the two ranges at Cottage Grove (Franklin and Dyrness 1973). While average yearly rainfall in the Cascades and Coast Range averages 200 to 340 cm, only about 100 cm falls in the Willamette Valley, and potential evapotranspiration far exceeds winter moisture buildup due to hot, dry summers (Habeck 1961; Franklin and Dyrness 1973).

The Willamette Valley is a mosaic of deciduous and coniferous forests, savannahs, grasslands, and wetlands (Johannessen et al. 1971; Franklin and Dyrness 1973). Oak forests and savannahs are dominated by *Quercus garryana* Hook. *Acer macrophyllum* Pursh, *Pseudotsuga menziesii* (Mirbel) Franco, and *Arbutus menziesii* Pursh may be co-dominant. *Pseudotsuga menziesii* dominates in coniferous forests, but *Abies grandis* (Douglas) Lindley and *A. macrophyllum* are also widespread. *Fraxinus latifolia* Benth. forests are common in seasonally flooded areas, especially along streams.

Prairies occupied extensive tracts of the Willamette Valley before it was settled; they are still widespread but now harbor many exotic species (Habeck 1961; Franklin and Dyrness 1973). These pre-settlement Willamette Valley prairies and savannahs may have been seral communities created and maintained by fire (Habeck 1961; Johannessen et al. 1971). Fire control has permitted the development of oak forests, and nearly all of the remaining prairie is currently being used for agriculture or grazing (Habeck 1961; Johannessen et al. 1971).

METHODS

Study Area. William L. Finley National Wildlife Refuge comprises 2156 hectares (5325 acres) about 14 km south of Corvallis, Benton County, OR, in the Willamette Valley. Elevations vary from 77 to 189 m (255 to 620 ft). Several pre-settlement Willamette Valley plant communities are preserved within the refuge. Forests, oak savannahs, native wet prairies, swamps, and marshes are interspersed with agricultural fields of wildlife food and cover crops, which together make up 25% of the total area. Both pre-settlement and settler-altered vegetation are represented. The refuge was established primarily as habitat for dusky Canada geese, the southern population of which winters almost exclusively in the Willamette Valley (Palmer 1976). All other native plant and animal species are protected as well. Human perturbations are uncommon outside of agriculture and of road building and maintenance and are strictly controlled.

Several Willamette Valley bryophyte substrates are especially well preserved at the refuge. Willamette Valley native wet prairie is a substrate now unique to Finley Refuge and only a few other sites. In these prairies, soil accumulation around graminoid hummocks forms vertical surfaces saturated during the winter but desiccated in summer. Forest

substrates include the bark of oaks and maples up to 250 years old, rotting logs and stumps, and forest floor litter and soil. Weathered rocks and cervid bones and antlers remain undisturbed in forests. Freshly dug forest, edge, and upland prairie soil is often present because moles, gophers, and voles are not artificially controlled. The bark of isolated oaks in savannahs and agricultural fields support a bryophyte assemblage distinct from that of forests. Vernal pool conditions are common in agricultural fields because wildlife food crop fields are worked in late summer or fall, rather than in spring as commercial agricultural crops are, leaving poorly drained areas undisturbed through spring and early summer. In addition, swamp mud, wet rocks or branches in and near streams, seasonally flooded shaded soil along streams, and upland grasslands are well represented. Because some roads are rarely used or maintained, roadbeds and compacted gravel remain undisturbed for long periods. Pigeon Butte, a sandstone hill bounded on the south by a basalt dike, provides both naturally exposed and quarried basalt. Scattered basalt boulders are also present on other hilltops.

Bryophyte Inventory. From February 1993 through August 1999, Finley Refuge was traversed on foot for the purpose of collecting bryophytes to make as complete an inventory as possible. Specimens were collected from all known substrates in all natural and human-influenced systems. The vascular plant community and substrate of each specimen was recorded. Except as otherwise noted, collections were identified by K. Merrifield using standard taxonomic works (Howe 1899; Schuster 1969; Lawton 1971; Schuster 1974; Schuster 1977; Crum and Anderson 1981; Smith 1990; Christy and Wagner 1996). Taxa newly or rarely reported for Oregon were confirmed or corrected by one or more of the following: W. F. Schofield and J. Harpel of the University of British Columbia, J. Christy of the Oregon Natural Heritage Program, and V. Bryan of Duke University. Voucher specimens of each species, and of each variety where applicable, as well as additional specimens from varying substrates, were placed in the Oregon State University Herbarium (OSC). Duplicate specimens were placed in the cryptogamic collection at Finley Refuge.

RESULTS

The bryophyte flora of Finley Refuge consists of 108 species, including 84 moss and 24 liverwort species, and 67 genera, including 52 moss and 15 liverwort genera. At least one hornwort, *Anthoceros* sp. *sensu latu,* was present. The largest moss family was Brachytheciaceae, represented by 14 species, followed by Bryaceae (8 species), Pottiaceae (8 species), Grimmiaceae (7 species), Dicranaceae (6 species), and Mniaceae (6 species). The largest liverwort family was Lophocoleaceae, represented by 5 species, followed by Jubulaceae and Porellaceae (3 species each.)

Physcomitrella patens (Hedwig) Bruch, Schimper & Gümbel is reported for the first time in Oregon in this study. Collections of *Syntrichia laevipila* Bridel var. *meridionalis* (Schimper) Juratzka made during this study along with collections from additional Willamette Valley localities were newly reported for Oregon earlier (Merrifield 2000). *Physcomitrium immersum* Sullivant and *Ephemerum serratum* (Hedwig) Hampe are both reported here for the second time in Oregon (Conard 1944; Christy 1980).

As of 1982, the known moss flora of Oregon comprised 411 species in 134 genera (Christy et al. 1982). About 20% of the statewide assemblage of moss species representing 39% of Oregon genera reside at Finley Refuge. Chapman and Sanborn (1941) documented 114 moss species in 60 genera in the entire Willamette Valley; 74% as many species and 87% as many genera were identified in this study. The known liverwort flora of Oregon comprises 168 species in 57 genera (D. H. Wagner unpublished) About 14% of the statewide assemblage of liverwort species representing 26% of Oregon genera were documented at Finley Refuge. Sanborn (1929) listed 116 liverwort species in 35 genera throughout western Oregon; 21% as many species and 43% as many genera were identified at Finley Refuge in this study.

DISCUSSION

Bryophyte diversity increases as the number of suitable substrates increases (Slack 1977). In western Oregon Cascade and Coast Range sites, increased forest floor bryophyte diversity was positively correlated with the abundance of rocks, coarse woody debris, stand openings, and hardwoods (Rambo and Muir 1998). Hardwoods such as red alder and bigleaf maple often support rich epiphytic bryofloras that differ from those on conifers (Christy and Wagner 1996). Rainfall dripping through hardwoods is richer in nutrients than that of conifers, and hardwoods allow greater light transmittance than do conifers (Rambo and Muir 1998). In forests alone at Finley Refuge, therefore, several factors encouraging bryophyte diversity are present: deciduous forests are more extensive than coniferous, rocks are present, variously decomposed coarse woody debris is plentiful, and stand openings as well as edges are common. Oak savannahs, wetlands, and riparian communities contribute additional diverse substrates under a variety of conditions.

Forests. All 6 bryophyte species occurring on forest floor litter and soil were common at Finley Refuge. *Rhytidiadelphus triquetrus* was the most abundant, and it dominated the herbaceous layer in many areas. In addition, the branches of *Trachy-*

TABLE 1.   TREE SUBSTRATES FOR BRYOPHYTES AT FINLEY REFUGE.

Latin name	Common name
Acer circinatum Pursh	Vine maple
Acer macrophyllum Pursh	Bigleaf maple
Alnus rubra Bongard	Red alder
Crataegus douglasii Lindley	Western hawthorne
Fraxinus latifolia Bentham	Oregon ash
Physocarpus capitatus (Pursh) Kuntze	Ninebark
Populus balsamifera L. spp. *trichocarpa* (Torrey & Gray) Brayshaw	Black cottonwood
Pseudotsuga menziesii (Mirbel) Franco	Douglas fir
Quercus garryana Hooker	Oregon white oak; Garry oak
Salix spp.	Willow

bryum megaptilum adhered to litter, although plants originated on freshly dug forest soil.

Rotting logs harbored 37 species. Among the most abundant were *Antitrichia californica, Aulacomnium androgynum, Brachythecium frigidum, Dicranoweisia cirrata, Eurhynchium praelongum* var. *stokesii, Homalothecium fulgescens, Hypnum subimponens, Isothecium myosuroides, Plagiomnium venustum, Cephalozia bicuspidata,* and *C. lunulifolia.* The rotting log bryophyte assemblage is expected to contain a high proportion of the liverwort flora in the spruce-fir biome of North America (Schuster 1969, 1974, 1977; Christy and Wagner 1996). Accordingly, 8 liverwort species in the genera *Cephalozia, Cephaloziella, Lepidozia, Lophocolea,* and *Scapania,* comprising 33% of the hepatic flora at Finley Refuge, were observed solely on rotting logs and branches.

The bark of living trees (Table 1) provided substrate for 35 species. *Antitrichia californica, Dendroalsia abietina, Dicranoweisia cirrata, Homalothecium fulgescens, H. nuttallii, Hypnum subimponens, Metaneckera menziesii, Neckera douglasii, Orthotrichum consimile, O. lyellii, Plagiomnium venustum, Porella navicularis,* and *P. roellii* were the most common. Bryophytes on shaded bark usually formed a continuous mat, while those that occurred on more exposed bark usually grew in small groups or discreet tufts. A solid mat of *M. menziesii* was especially characteristic of large forest oaks.

Isolated Oaks. The bryophyte assemblage of exposed, often sparsely shaded bark of isolated oaks comprised an unidentified, nonsporulating *Didymodon* species, *Dicranoweisia cirrata, Syntrichia ruralis, S. latifolia, S. laevipila* var. *meridionalis,* and *Zygodon viridissimus,* the latter three of which are gemmiparous (Merrifield 2000). In some collections in which *S. laevipila* var. *meridionalis* gametophores were not found, its gemmae were present among the other mosses. Areas where some or all of these 6 taxa coalesced were colonized by mosses more characteristic of shaded bark, such as *Homalothecium nuttallii, Metaneckera menziesii,* and *Dendroalsia abietina.*

Upland Soils. Thirty-eight bryophyte species occurred on soils. Disturbed, packed upland soil and soil freshly disturbed by small mammals each harbored 9 species; *Tortula atheroides* and *Scleropodium touretii* were common to both. *Trachybryum megaptilum* grew on mammal-dug forest soil. Only three bryophyte species, *Brachythecium albicans, Bryum lisae* var. *cuspidatum,* and *Dicranum scoparium,* inhabited upland prairie soils. The occurrence of the first two were limited. In contrast, extensive collections from many prairie localities indicated that *Brachythecium albicans* is a widespread and profuse grassland community component.

Because agricultural fields occupy about 25% of Finley Refuge land, and because some fields lie fallow for long periods, exposed agricultural soil is extensive. Of the three moss species inhabiting upland agricultural soils, *Bryum dichotomum* was by far the most abundant, covering vast expanses of soil unworked in spring.

Wetland Soils. Cumulative losses of bryophyte taxa in western Oregon, Washington, and California have probably been greatest for the wet soil species occurring on floodplains, where agricultural impacts have been concentrated (Christy and Wagner 1996). Due to preservation of several native wetland habitats and to crop management for wildlife rather than for market consumption, including leaving poorly drained field soils comparatively undisturbed, Finley Refuge continues to harbor elements of this bryophyte assemblage.

Several soil substrates were seasonally flooded. Primary succession on such recently disturbed soil includes many opportunistic bryophyte species (Christy and Wagner 1996). Both flat streamside soils and undrained soils in agricultural fields harbored vascular plants characteristic of vernal pools. *Physcomitrella patens, Leptodictyum riparium,* and *Riccia fluitans* were unique to streamsides. *Dicranella heteromalla, Pohlia annotina,* and *Fossombronia wondraczekii* were unique to low, undrained areas in cultivated fields, and *Physcomitrium pyriforme* occurred on both streamsides and undrained field soils. Several *Riccia* species from undrained soils remain to be identified (J. Wheeler personal communication). *Riccia fluitans* and *Ricciocarpus natans* were the only two free-floating species, and

they were also found stranded on streamside mud. *Ditrichum schimperi, Ephemerum serratum,* and a depauperate form of *Philonotis fontana* were unique to seasonally flooded native wet prairie vertical soil surfaces of graminoid hummocks. *Plagiomnium medium* and *P. ellipticum* were unique to the seasonally flooded mud of ash swamps.

Permanently shaded vertical soil surfaces along streams supported a unique bryophyte assemblage, including *Atrichum selwynii, Eurhynchium praelongum* var. *praelongum, Fissidens bryoides, Jungermannia rubra,* and *Riccardia multifida.*

Rocks, Bones, and Antlers. Basalt provided substrate for 30 species. The most common included *Dicranoweisia cirrata, Didymodon vinealis, Grimmia pulvinata, G. trichophylla, Homalothecium nuttallii, Orthotrichum lyellii, Racomitrium canescens,* and *R. heterostichum.* While a distinctive assemblage of Pacific Northwest bryophyte species occurs on rocks (Christy and Wagner 1996), some rock-dwelling species at Finley Refuge also occurred on other substrates. Overlap occurred among rotting log-, bark-, and basalt-dwellers, but only *Antitrichia californica, D. cirrata,* and *I. myosuroides* occurred on all three.

None of the moss species on basalt were among the 5 on weathered sandstone, which included *Fissidens bryoides* and *Scleropodium touretii,* also inhabitants of disturbed upland soils. Fifteen moss species occurred on concrete, and this was the only substrate on which *Amblystegium serpens* and *Tortula muralis* were found. No species were found on both concrete and sandstone. Only *Brachythecium frigidum, Eurhynchium praelongum* var. *praelongum,* and *Sanionia uncinata* occurred on bone and antler.

Bryophytes Expected but Uncommon or Absent. *Antitrichia curtipendula, Claopodium crispifolium, Scapania bolanderi,* and *Isothecium myosuroides* were less common than expected judging from accounts of Pacific Northwest bryoflora (Lawton 1971, Schofield 1976, Vitt et al. 1988). The first three were found only on forested north-facing slopes in isolated patches rather than broad mats. *Antitrichia curtipendula* requires humidity and is considered closely associated with late successional or old-growth forests (Schofield 1976, FEMAT 1993, Christy and Wagner 1996), but Chapman and Sanborn (1941) collected *A. curtipendula* as well as *C. crispifolium* throughout the Willamette Valley. *Scapania bolanderi* has often been collected in coastal regions (Howe 1899, Vitt et al. 1988) and Cascade slopes (Sanborn 1929) and is also considered closely associated with late-successional or old-growth forests (FEMAT 1993). *Isothecium myosuroides* was widespread at Finley Refuge but did not dominate forest epiphytes as it does at some Coast Range sites (Peck 1997).

Two mosses that were expected but not found at Finley Refuge were *Rhytidiadelphus loreus* (Hedwig) and *Hylocomium splendens* (Hedwig) Bruch, Schimper & Gümbel. Most of Chapman and Sanborn's (1941) collections of *R. loreus* were from the humid margins of the Willamette Valley, but their collections of *H. splendens* were on substrates and at elevations comparable to those at Finley Refuge. The absence of these species in this study may be a function of the relatively dry climate of the Willamette Valley or of this particular locality.

At Finley Refuge, land managed primarily for wildlife and for protection of natural systems preserves a variety of native and settler-altered plant communities that provide a wide range of substrates, resulting in a diverse and abundant bryophyte assemblage.

Annotated Species List

All substrates on which each taxon was found are listed. Moss nomenclature follows that of Anderson et al. (1990), except for that of Pottiaceae, which follow Zander (1993), and *Eurhynchium,* which follows Lawton (1971). Liverwort nomenclature follows that of Stotler and Crandall-Stotler (1977). Numbers following taxa and descriptions are Merrifield collection numbers retained as vouchers in OSC. The number followed by RH is a Richard Halse collection number.

Class Musci

Amblystegium serpens (Hedwig) Bruch, Schimper & Gümbel var. *juratzkanum* (Schimper) Rau & Hervey [Amblystegiaceae]. Concrete. *932c.*

Antitrichia californica Sullivant *in* Lesquereux [Leucodontaceae]. Bark of Oregon white oak, willow sp., and black cottonwood; rotting deciduous log, burned log, exposed basalt, shaded basalt, concrete. *605, 610, 1179.*

Antitrichia curtipendula (Hedwig) Bridel [Leucodontaceae]. Bark of Douglas fir and red alder, rotting vine maple; unidentified rock; all deeply shaded. *1181.*

Atrichum selwynii Austin [Polytrichaceae]. Stream-cut bare soil bank. *1383.*

Aulacomnium androgynum (Hedwig) Schwaegrichen [Aulacomniaceae]. Bigleaf maple log, unidentified deciduous log, basalt. *632, 651.*

Brachythecium albicans (Hedwig) Schimper in Bruch, Schimper & Gümbel [Brachytheciaceae]. Soil among grass in savannah, upland grasslands, and lawn; packed soil; shaded basalt. *966, 977, 1700c.*

Brachythecium frigidum (C. Müller) Bescherelle [Brachytheciaceae]. Rotting bigleaf maple log, butt of rotting bigleaf maple, damp log in streambed, weathered unidentified rock, permanently shaded basalt in depression below soil line, shaded basalt above ground, clay soil among emergents, mud among *Carex* under Oregon white oak and Oregon ash, clay soil among emergents, fallen branch in mud, deer skull and antlers,

Gandoderma-complex fruiting structure on log. *871, 979, 1187, 1418, 1692.*

Brachythecium rivulare Schimper *in* Bruch, Schimper & Gümbel [Brachytheciaceae]. Moist, shaded basalt; dry, exposed rock; rock in flowing water; mud among *Carex* under Oregon white oak and Oregon ash; rotting bigleaf maple log; white-rotted standing bigleaf maple butt. *674, 677, 974, 975, 1385b.*

Bryum argenteum Hedwig [Bryaceae]. Totally unshaded basalt in natural outcrop. *1428.*

Bryum caespiticum Hedwig [Bryaceae]. Agricultural field soil. *1224.*

Bryum canariense Bridel [Bryaceae]. Basalt, concrete, soil over concrete, soil between rocks in gravel road. *791.*

Bryum capillare Hedwig [Bryaceae]. Rotting log, weathered stump roots, soil between uprooted tree roots, concrete, shaded basalt, packed soil, hummock in wet prairie. *649, 943, 1700b.*

Bryum dichotomum Hedwig [Bryaceae]. Packed soil at agricultural field edge, disturbed soil among grass at field edge, packed road soil. *1222, 1227b.*

Bryum lisae De Notaris var. *cuspidatum* (Bruch, Schimper & Gümbel) Margot [Bryaceae]. Concrete, packed soil among grasses. *932b.*

Ceratodon purpureus (Hedwig) Bridel [Ditrichaceae]. Exposed basalt, shaded basalt, packed soil. *785, 962.*

Claopodium crispifolium (Hooker) Renauld & Cardot [Leskeaceae]. Bigleaf maple bark and weathered sandstone, both deeply shaded. *1175.*

Dendroalsia abietina (Hooker) Britton [Leucodontaceae]. Rotting deciduous and Douglas fir logs; bark of Oregon white oak, Douglas fir and black cottonwood bark. *609.*

Dicranella heteromalla (Hedwig) Schimper [Dicranaceae]. Drying undrained agricultural soil. *1459b.*

Dicranoweisia cirrata (Hedwig) Lindberg *ex.* Milde [Dicranaceae]. Oregon white oak bark, rotting Oregon white oak log, burned log, split wood fenceposts, basalt, packed road soil. *620, 623, 1227a.*

Dicranum fuscescens Turner [Dicranaceae]. Rotting Douglas fir bark. *661, 681.*

Dicranum howellii Renauld & Cardot [Dicranaceae]. Rotting Oregon white oak, rotting bigleaf maple stump, bigleaf maple bark. *621, 1178.*

Dicranum scoparium Hedwig [Dicranaceae]. Rotting bigleaf maple stump, soil among grasses. *660a, 1687.*

Dicranum tauricum Sapehin [Dicranaceae]. Sides and cross section of rotting bigleaf maple and Douglas fir stumps. *681a.*

Didymodon vinealis (Bridel) Zander [Pottiaceae]. Concrete, freshly disturbed soil, exposed basalt. *934b, 951.*

Didymodon sp. [Pottiaceae]. Bark of isolated Oregon white oaks. *1676b.*

Ditrichum shimperi (Lesquereux) Kuntze [Ditrichaceae]. Shaded soil of native wet prairie hummock. *1572.*

Ephemerum serratum (Hedwig) Hampe [Ephemeraceae]. Soil of hummock in native prairie. *1570* [det. by V. Bryan].

Eurhynchium oreganum (Sullivant) Jaeger [Brachytheciaceae]. Vine maple bark, rotting Douglas fir log, Douglas fir butt, basalt, soil over rock. *617.*

Eurhynchium praelongum (Hedwig) Bruch, Schimper & Gümbel var. *praelongum* [Brachytheciaceae]. Woody debris among *Carex*, creekbank soil, damp upland soil, ash swale soil, shaded weathered sandstone, concrete, gravel in flowing stream, lawn, branches in stream splash zone, ninebark root in dry streambed, butt of bigleaf maple log, deer skull and antlers. *634, 984b.*

Eurhynchium praelongum (Hedwig) Bruch, Schimper & Gümbel var. *stokesii* Turner [Brachytheciaceae]. Rotting Oregon white oak, butt of bigleaf maple log, forest floor litter. *613, 1212.*

Fissidens bryoides Hedwig [Fissidentaceae]. Clay stream bank, freshly disturbed soil, weathered sandstone, ditch at field edge. *874, 877, 1186, 1287.*

Fontanalis antipyretica Hedwig var *antipyretica* [Fontinalaceae]. Rocks in flowing water, submerged tree root, ninebark root in dry streambed. *1185.*

Funaria hygrometrica Hedwig [Funariaceae]. Burned soil, burned wood, weathered stump roots, agricultural field soil, mud. *835.*

Grimmia incurva Schwaegrichen [Grimmiaceae]. Exposed basalt. *1424.*

Grimmia pulvinata (Hedwig) Smith [Grimmiaceae]. Basalt, concrete. *782, 1048, 1682b.*

Grimmia trichophylla Greville [Grimmiaceae]. Basalt, concrete. *783, 942, 952, 1046, 1057, 1431.*

Homalothecium aeneum (Mitten) Lawton [Brachytheciaceae]. Exposed basalt. *790.*

Homalothecium fulgescens (Mitten *ex* C. Müller) Lawton [Brachytheciaceae]. Bark of bigleaf maple, hawthorne, Oregon ash, and Oregon white oak; fallen bigleaf maple branches, rotting unidentified log, rotting lumber, exposed rock, shaded basalt, concrete. *643, 666, 673a, 1054, 1690.*

Homalothecium nuttallii (Wilson) Jaeger [Brachytheciaceae]. Bark of western hawthorne, black cottonwood and Oregon white oak; burned log, exposed unidentified rock, basalt, concrete, freshly disturbed soil. *616, 673b, 680.*

Hypnum circinale Hooker [Hypnaceae]. Rotting Oregon white oak and unidentified stump, Oregon ash bark, rotting stump, exposed unidentified rock. *625, 1210.*

Hypnum subimponens Lesquereux [Hypnaceae]. Basalt, rotting Oregon ash and unidentified logs and branches, Oregon ash bark, bigleaf maple butt, shaded basalt. *1183, 1188, 1691.*

Isothecium cristatum (Hampe) Robinson [Brachytheciaceae]. Douglas fir bark; Douglas fir and unidentified stumps; rotting Oregon white oak, bigleaf maple, and unidentified logs. *644, 662, 1189, 1216.*

Isothecium myosuroides Bridel [Brachytheciaceae]. Bark of Oregon ash, Douglas fir and Oregon white oak, rotting Oregon white oak and bigleaf maple logs, rotting branches of Douglas fir and Oregon ash, unidentified rock. *612, 1172.*

Leptobryum pyriforme (Hedwig) Wilson [Bryaceae]. Freshly disturbed soil. *988d.*

Leptodictyum riparium (Hedwig) Warnstorf [Amblystegiaceae]; soil in and near stream at agricultural field edge. *669.*

Leucolepis acanthoneuron (Schwaegrichen) Lindberg [Mniaceae]. Oregon ash roots, rotting bigleaf maple and Douglas fir logs, basalt, shaded weathering sandstone, shaded soil. *635, 1060.*

Metaneckera menziesii (Hooker *in* Drummond) Steere [Neckeraceae]. Bark of bigleaf maple, Oregon ash, and Oregon white oak. *1231.*

Neckera douglasii Hooker [Neckeraceae]. Oregon white oak bark, Douglas fir branches, unidentified rock. *611.*

Orthotrichum consimile Mitten [Orthotrichaceae]. Recently fallen Oregon ash and unidentified branches, burned log, basalt, concrete. *633, 1157a, 1158, 1288.*

Orthotrichum lyellii Hooker and Taylor [Orthotrichaceae]. Bark of bigleaf maple, western hawthorne, Oregon ash, black cottonwood, Oregon white oak, burned log, basalt, shaded basalt. *615, 1058, 1157, 1265.*

Orthotrichum speciosum Nees *ex* Sturm [Orthotrichaceae]. Black cottonwood bark. *1113.*

Philonotis fontana (Hedwig) Bridel [Bartramiaceae]. Side of mud hummock in wet prairie; one small collection of depauperate specimen. *1569.*

Physcomitrella patens (Hedwig) Bruch & Schimper *in* Bruch, Schimper & Gümbel [Funariaceae]. Shaded mud under bridge. *1156a* [det confirmed by J. Christy].

Physcomitrium immersum Sullivant [Funariaceae]. Shaded mud along streams and under bridge, streamside mud. *1156b* [det. confirmed by W. B. Schofield].

Physcomitrium pyriforme (Hedwig) Hampe [Funariaceae]. Packed mud, drying undrained agricultural soil. *1410.*

Plagiomnium ellipticum (Bridel) T. Koponen [Mniaceae]. Clay soil under Oregon ash. *872.*

Plagiomnium insigne (Mitten) T. Koponen [Mniaceae]. Rotting bigleaf maple, Douglas fir, and unidentified logs, unidentified rock near stream, forest soil, gravity-disturbed soil bank. *655c, 671, 686, 982, 1117, 1190, 1219.*

Plagiomnium medium (Brusch & Schimper in Bruch, Schimper & Gümbel) T. Koponen [Mniaceae]. Clay soil under Oregon ash. *1159, 1168.*

Plagiomnium venustum (Mitten) T. Koponen [Mni-

aceae]. Bark of Oregon ash and Oregon white oak, rotting bigleaf maple and Oregon white oak logs, exposed basalt, shaded basalt, unidentified rock. *606, 622, 1050.*

Plagiothecium laetum Schimper *in* Bruch, Schimper & Gümbel [Plagiotheciaceae]. Rotting bigleaf maple and unidentified deciduous log. *631, 659.*

Pleuridium subulatum (Hedwig) Rabenhorst [Ditrichaceae]. Freshly disturbed soil. *988b.*

Pohlia annotina (Hedwig) Lindberg [Bryaceae]. Drying undrained agricultural soil. *1455, 1561.*

Polytrichum juniperinum Hedwig [Polytrichaceae]. Overgrown roadbed, exposed basalt, soil in depression in shaded basalt. *780, 1045.*

Polytrichum piliferum Hedwig [Polytrichaceae]. Exposed basalt. *1434.*

Pterogonium gracile (Hedwig) Smith [Anomodontaceae]. Oregon white oak bark, fallen angiosperm bark, barkless Oregon white oak log, unidentified rotting log. *612, 648, 1416, 1673.*

Ptycomitrium gardneri Lesquereux [Ptychomitriaceae]. Basalt. *1043, 1051.*

Racomitrium canescens (Hedwig) Bridel [Grimmiaceae]. Overgrown gravel roadbed, rocky soil, basalt. *779, 1044.*

Racomitrium heterostichum (Hedwig) Bridel [Grimmiaceae]. Dry, exposed basalt; shaded basalt, and unidentified rock. *672, 788, 1385, 1433, 1696.*

Racomitrium occidentale (Renauld & Cardot) Renauld & Cardot [Grimmiaceae]. Partially shaded basalt. *1053.*

Rhizomnium glabrescens (Kindberg) T. Koponen [Mniaceae]. Unidentified rotting log. *1114.*

Rhytidiadelphus triquetrus (Hedwig) Warnstorf [Hylocomiaceae]. Deciduous sapling bark, Oregon ash bark, forest floor litter, shaded basalt, soil over rock. *619.*

Sanionia uncinata (Hedwig) Loeske [Amblystegiaceae]. Rotting Oregon ash branch, shaded wooden bridge support, shaded deer skull and antlers on forest floor. *1167, 1382.*

Schistidium apocarpum (Hedwig) Brusch & Schimper in Bruch, Schimper & Gümbel [Grimmiaceae]. Shaded basalt. *1689.*

Scleropodium cespitans (C. Müller) L. Koch [Brachytheciaceae]. Oregon white oak upper branch and butt bark. *1284b, 1678, 1681, 1683.*

Scleropodium obtusifolium (Jaeger) Kindberg in Macoun & Kindberg [Brachytheciaceae]. Streambed gravel. *984a, 972, 1220.*

Scleropodium touretii (Bridel) L. Koch var *touretii* [Brachytheciaceae]. Packed soil, disturbed loose forest soil, shaded weathered sandstone, soil among road rocks. *960, 976, 985, 1195.*

Syntrichia laevipila Bridel var. *laevipila* [Pottiaceae]. Bark of Oregon white oak in small, open group in agricultural fields and savannahs. With the var. *laevipila, 1198, 1684a, 1685a, 1685b.*

Syntrichia laevipila Bridel var. *meridionalis*

(Schimper) Juratzka [Pottiaceae]. Bark of isolated Oregon white oak in agricultural fields and savannahs, with var. *laevipila*. *1198, 1684a, 1685a, 1685b* [det. confirmed by J. Harpel].

Syntrichia latifolia (Hartman) Hübener [Pottiaceae]. Oregon white oak bark, shaded concrete. *946, 1197, 1684b, 1685b.*

Syntrichia princeps (De Notaris) Mitten [Pottiaceae]. Oregon white oak bark, weathered stump roots, basalt, burned log, concrete. *930, 951, 1049, 1284a.*

Syntrichia ruralis (Hedwig) Weber & Mohr [Pottiaceae]. Basalt, Oregon white oak bark, especially in savannahs. *1059, 1677b, 1685c, 1686.*

Tetraphis pellucida Hedwig [Tetraphidaceae]. Rotting bigleaf maple log. *658.*

Timiella crassinervis (Hampe) L. Koch [Pottiaceae]. Freshly disturbed partially shaded soil. *988c.*

Tortula atheroides Zander [Pottiaceae]. Packed soil, freshly disturbed soil. *963, 990.*

Tortula muralis Hedwig [Pottiaceae]. Concrete. *954.*

Trachybryum megaptilum (Sullivant) Schofield [Brachytheciaceae]. Disturbed forest soil, forest floor litter, exposed rotting wood and adjacent disturbed soil, exposed concrete. *980, 981a.*

Zygodon viridissimus (Dickson) Bridel var. *viridissimus* [Orthotrichaceae]. Savannah oak bark. *1675a, 1677a.*

Class Hepaticae

Cephalozia bicuspidata (L.) Dumortier [Cephaloziaceae]. Rotting unidentified log, among mosses on basalt, on and among *Didymodon* sp. on savannah oak bark. *882.*

Cephalozia lunulifolia (Dumortier) Dumortier [Cephaloziaceae]. Rotting bigleaf maple log. *655a.*

Cephaloziellaceae divaricata (Smith) Schiffner [Cephaloziellaceae]. Rotting bigleaf maple log. *654a.*

Chyloscyphus polyanthos (L.) Corda var. *polyanthos* [Lophocoleaceae]. Bare soil in Oregon ash swale, on soil among *Carex* sp. under Oregon white oak and Oregon ash. *870.*

Chyloscyphus polyanthos (L.) Corda var. *rivularis* (Schrader) Nees [Lophocoleaceae]. Streambed. *668.*

Fossombronia wondraczekii (Corda) Dumortier [Codoniaceae]. Drying undrained agricultural soil. *1560.*

Frullania bolanderi Austin [Jubulaceae]. Oregon white oak bark. *624.*

Frullania californica (Austin) Evans [Jubulaceae]. Oregon white oak bark. *925.*

Frullania tamarisci (L.) Dumort ssp. *nisquallensis* (Sullivant) Hattori [Jubulaceae]. Oregon ash bark, Douglas fir bark. *636, 1115.*

Jungermannia rubra Gottsche *ex* Underwood [Lophoziaceae]. Streambank mud. *878.*

Lepidozia reptans (L.) Dumortier [Lepidoziaceae]. Rotting stump. *1209.*

Lophocolea bidentata (L.) Dumortier [Lophocoleaceae]. Rotting bigleaf maple; rotting unidentified logs and branches. *653, 1381.*

Lophocolea cuspidata (Nees) Limpricht [Lophocoleaceae]. Rotting unidentified log. *881.*

Lophocolea heterophylla (Schrader) Dumortier [Lophocoleaceae]. Rotting bigleaf maple log, rotting unidentified stump. *655b, 1213.*

Marchantia polymorpha L. [Marchantiaceae]. Perpetually wet concrete, soil in ash swale, moist disturbed agricultural soil. *1221,* RH *4729.*

Porella cordeana (Hübener) Moore [Porellaceae]. Among *Rhytidiadelphus triquetrus* among rocks over soil, concrete in ephemeral streambed. *987, 1384.*

Porella navicularis (Lehmann et. Lindenberg) Lindberg [Porellaceae]. Bark of Oregon white oak, Oregon ash, and Douglas fir; exposed basalt; shaded basalt. *603, 1116.*

Porella roellii Stephani [Porellaceae]. Oregon white oak bark, rotting bigleaf maple log. *604, 613.*

Radula bolanderi Gottsche [Radulaceae]. Douglas fir bark. *645.*

Radula complanata (L.) Dumortier [Radulaceae]. Oregon ash bark; vine maple bark; rotting branch. *640, 685, 968a.*

Riccardia multifida (L.) S. Gray [Aneuraceae]. Crumbling undercut creekbank soil. *876.*

Riccia spp. [Ricciaceae]. Undrained agricultural soils. *1565a, 1565b.*

Riccia fluitans L. [Ricciaceae]. Streamside mud. *1153.*

Ricciocarpus natans (L.) Corda [Ricciaceae]. Free-floating, shaded mud. *869, 884.*

Scapania bolanderi Austin [Scapaniaceae]. Rotting stump on north-facing forested slope. *1208.*

Scapania umbrosa (Schrader) Dumortier [Scapaniaceae]. Rotting Oregon white oak branch on north-facing forested slope. *1437.*

Class Anthocerotae

Anthoceros sensu latu sp. [Anthocereotaceae]. North underhand of *Juncus* hummock in native wet prairie. *1568.*

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EVIDENCE FOR A SAND HILLS ECOTYPE OF *ESCHSCHOLZIA CALIFORNICA* (PAPAVERACEAE)

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Abstract

The *Eschscholzia californica* Cham. growing in the Ben Lomond sand hills in the Santa Cruz mountains appears different from other populations in the surrounding areas. To quantify these differences, populations in coastal, sand hills, and serpentine soils were compared. Phenotypic data were collected from the field in 1998 and 1999. A common garden experiment was also performed. Differences in torus rim width, flower color, flower number, and leaf coloration were examined in both the field and the common garden. The sand hills population was different from both the coastal and the serpentine populations for leaf coloration. Population differentiation occurred among all three sites for at least some of the floral characters examined. The common garden experiment indicates that some of the differences among the populations are phenotypically stable.

Introduction

The Ben Lomond sand hills are a textbook example of the geographic factors that give rise to endemism (Mayer et al. 1994; Kruckeberg 1986). Isolated intrusions of dry sandy soil and associated drought-adapted plant communities are in stark contrast to the damp redwood forest surrounding the sand hills. Edaphic habitat disjunction can cause parapatric speciation (Kruckeberg 1954; Proctor and Wodell 1975). In the case of *Eschscholzia californica* Cham., a species that is found in open, disturbed habitats, populations in the sand hills may be isolated by large regions of dense forest habitat, eventually leading to allopatric speciation. Isolation and soil-specific adaptation can produce a great degree of population differentiation in a short period of time (Proctor and Wodell 1975).

A more common example of edaphic factors associated with endemism in the California flora is the presence of serpentine-adapted communities throughout the state. Serpentine adaptation is not treated consistently in taxonomic terms. In some cases, a serpentine-adapted group of populations is recognized as a separate subspecies (e.g., *Streptanthus insignis* Jepson ssp. *lyonii* Kruckeb. & J. Morrison) and, in other cases, it is grouped with serpentine-intolerant populations (e.g., *Streptanthus glandulosus* Hook.) (Kruckeberg 1986).

Eschscholzia californica is known for its local variation. By the early part of this century, over 90 varieties of had been described (Greene 1905). The 90 varieties were reduced to four by Munz and Keck (1968). They recognized coastal, central, southern, and dune varieties in California. *Eschscholzia californica* is known for its plasticity

and is now found in open, semi-disturbed habitats all over the globe. Cook (1961) performed a survey of *E. californica* over the state of California and found local differentiation in self-compatibility, flower fertility, seed production, and stamen number. He found a graded mosaic pattern in the distribution of nearly all the phenotypic characters he measured. Although his work focused on populations west of the Central Valley, *E. californica* in Santa Clara and Santa Cruz counties were not included. This study examines local differentiation among 3 populations in 3 different habitats in the south San Francisco Bay Area: a serpentine habitat, an inland sand hill habitat, and a coastal meadow habitat. This study looks at differentiation among the populations in two ways: field phenotypic measurement (how the plants appear in their own habitat) and common garden phenotypic measurement (controlling environmental influence). The plants at the sand hills were of particular interest due to their vibrant purple leaves with large white spots. While the species is widely recognized to be variable in terms of floral morphology and growth habit, leaf color variation has not been formally described in this species before.

Local differentiation is a much-studied phenomenon because of its contribution to evolutionary and conservation theory (Waser and Price 1985; Montagnes and Vitt 1991; Mayer et al. 1994; Kindell et al. 1996; Linhart and Grant 1996). Finding how much field-observed population differences are in response to environmental factors requires some *ex situ* investigation. Common garden experiments are effective in determining the strength of the adaptation of each population to its own soil environment. By performing a common garden experiment rather than a reciprocal transplant experiment, we focused purely on soil environment and controlled confounding factors such as unequal responses to

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differences in interspecific competition and preda-
tion that may have existed within each population.
Also, by performing a common garden experiment
rather than a reciprocal transplant experiment, we
avoided the likelihood of polluting a possibly sen-
sitive habitat-adapted genome (at the sand hills)
with detrimental alleles.

Recognition of special, locally-adapted popula-
tions of plants has proved valuable in conservation
of fragile ecosystems. Most rare plant occurrences
in California are in mixed chaparral, grasslands,
coastal scrub, and valley-foothill woodland, yet in
terms of the percentage of total habitat preserved
(wilderness areas, research reserves, national and
state parks, wildlife refuges, and recreational sites)
alpine and sub-alpine areas are afforded propor-
tionally the most protection (Pavlik and Skinner
1994). While the identification of a rare plant in a
previously unknown area can ensure some protec-
tion (Bartel et al. 1994), Pavlik and Skinner (1994)
recommend promoting habitat-based conservation
plans, particularly in serpentinite, rocky, and sandy
substrates at non-alpine elevations that harbor the
highest degrees of overall endemism. The sand hills
are certainly a candidate for this type of protection:
California Department of Fish and Game has ex-
pressed interest in this area, and 9 of the 97 species
found in the sand hills are thought to be ecotypes,
with 8 additional species probably warranting ad-
ditional taxonomic study (Lee 1996).

METHODS

Study sites. In 1998, one coastal, one sand hills,
and one serpentine population were sampled. In
1999, two coastal, two sand hills, and one serpen-
tine population were sampled. Both coastal sites
were located at Wilder Ranch State Park, just north
of Santa Cruz. The sand hills sites were located in
a watershed ravine just off Mt. Hermon Road in
Scotts Valley. The property is privately owned and
previously contained a sand quarry. The serpentine
site is located on Tulare Hill in the Santa Teresa
Hills in the city of San Jose. The property is leased
for cattle grazing.

The coastal site sampled in both 1998 and 1999
(W1) is a tabletop meadow 0.4 km southwest of the
historic ranch buildings. The site is mowed every
summer, late in the flowering season. *Bromus hord-
caccus* L., *Raphanus sativus* L., and *Carduus pyc-
nocephalus* L. dominate this site. The coastal site
sampled in 1999 only (W2) was located 0.4 km east
of the historic ranch buildings. The species com-
position of this south-facing community was dom-
inated by *Bromus diandrus* Roth and *C. pycnoce-
phalus.* Although the sites are coastal, the *E. cali-
fornica* at this location does not fit the description
of the coastal "race" of *E. californica* (described
in Munz and Keck 1968), but rather the inland va-
riety. Due to the proximity of the sites to the ranch
house and gardens, it is possible that these popu-
lations are descendants of once-planted individuals.

The sand hills *E. californica* population sampled
in 1998 and 1999 (SH1) occurred on both the
south-facing and north-facing sides of the ravine.
The south-facing slope community contained a
grassland understory (*Briza maxima* L. dominant)
beneath scattered ponderosa pine. The north-facing
slope community consisted of spring flowering an-
nuals (*Lupinus bicolor* Lindley, *Gilia tenuiflora*
Benth., *Castilleja exserta* [A A Helbr.] Chuang &
Heckard) spread thinly over bare sand. The sand
hills site sampled in 1999 only (SH2) was on the
lower sloping face of a sand quarry scar 0.2 km
south of the first sand hills population. The scar
bends in a semi circle from south-facing to west-
facing slopes. Plants at SH2 flowered 5 weeks ear-
lier than those at SH1, and the community consisted
almost entirely of *E. californica* and *Lupinus albi-
frons* Benth.

The *E. californica* population on serpentine soil
(SERP) was sampled in both 1998 and 1999. The
population area is located on north- and east-facing
slopes in a serpentine grassland community con-
taining species such as *Avena fatua* L., *Hordeum
murinum* L. ssp. *leporinum* and *Lasthenia platyg-
lossa.*

Populations located on the same soil type were
close enough together that gene flow between them
is a distinct possibility. Differences in plant com-
munity composition and extremely low densities of
E. californica plants between the populations indi-
cated that separate treatment might be appropriate.
In all cases, the entire population of *E. californica*
was not measured, but rather a high-density lobe
within the population was sampled. Individual
plants of *E. californica* could be found at low den-
sities for thousands of meters from the sampling
areas. Sampling areas were defined by high *E. cal-
ifornica* concentration (generally more than 1 plant
per m^2), and also by artificial (fences, drainage
ditches) and geologic (cliffs and other drastic
changes in slope) barriers.

Field data collection. In 1998, 3 populations
were sampled for plant phenotypic characteristics.
Population W1 was sampled on June 26; SERP was
sampled on May 1; SH1 was sampled on July 1.
An effort was made to sample each population
when the largest numbers of plants were flowering.
Between 45 and 65 plants were randomly sampled
at each population. Data collected for each plant
were the number of floral units, leaf color, torus rim
width, and flower 1-color or bicolor. Floral units
were recorded as the number of flowers plus the
number of buds plus the number of capsules. Torus
rim width and flower color were measured on the
tallest flower. Torus rim width was taken at the wid-
est point and was recorded as either 1, 2, or 3 mm.

Flower color was recorded by comparing the
base to the tip of the petals on the flower on the
tallest branch. Obvious differences between the two
were considered to be evidence of the "bicolor"

character in the flower. If there appeared to be only a slight difference between the color of the tip of the petal compared to the base of the petal, or no difference at all, the flower was recorded as "1-color."

Leaf color data were collected by observing the color characteristics of the leaf: presence of white spots, visible presence of green pigmentation, visible presence of purple pigmentation, and presence of red tips on the leaf. Red-tipped leaves appear to be fairly common in *E. californica,* and almost all living leaves of the plant can be characterized as green. However, some leaves of *E. californica* have a purplish tinge that is found throughout the leaf. Where green was visible and tinged with purple, both the green leaved and the purple leaved character were marked as present. In some plants this purple color is so vibrant that no green color can be seen. In these plants, the purple-leaf character was recorded as present, and the green-leaf character was recorded as absent. In 1998, each character was noted as either present or absent for the third leaf from the top of the longest branch of each randomly selected plant.

Stanton Cook (1961) used flower color and torus rim width in his investigations of statewide variability in *E. californica.* Clark and Charest (1992) used number of floral units in their study of population differentiation in the Antelope Valley. Leaf color was of interest because of the apparent difference between the sand hills population for this character and the other two populations.

In 1999, 15 plants per population were sampled for floral characters to see if the differences observed among populations were consistent and if they would be present in two very different climatic years: El Niño and La Niña winters (NOAA 2000). Number of flower units, torus rim width and flower color were measured over time at sites W1, SH1, and SERP to make sure that differences observed in 1998 would be consistent within the season. Fifteen plants were sampled in each population every 2 weeks. The same sampling scheme was used for each data collection. Although it is unlikely that the same plants were measured on each sampling date, the plants were located in roughly the same areas. Sampling dates were April 1, April 15, April 28, May 12, May 27, and June 10.

Floral and leaf character data were collected at the estimated peak of flowering for W1 (April 15), W2 (May 13), SH1 (May 27), SH2 (April 22), and SERP (April 28). Instead of just looking at a single leaf of the plant, all of the leaves of the plant were examined for leaf color characters in 1999. Because no differences were found for this character in 1998, data on the red-tipped leaf character were not collected in 1999.

Common garden experiment. Seeds were collected from W1 and SH1 in July 1998 from 30 randomly selected plants in each population. The

TABLE 1.   DESIGN OF THE COMMON GARDEN EXPERIMENT.

Soil source	Seed source	# pots	# seeds/pot
SH1	SH1	16	9
W1	SH1	16	9
SH1	W1	11	6
W1	W1	11	6

seeds, identified by parent plant, were stored in paper envelopes until February 1999, at which time the seeds were placed in 10 cm × 10 cm pots filled with soil from the W1 and SH1 population areas. Only ripe seeds were used; collected seeds that were unripe were not used in the experiment. A total of 210 seeds from 11 plants from SH1 and 210 seeds from 6 plants from W1 were used in the experiment. In all but 2 pots, seeds from only 1 parent were sown per pot. Due to seed from some SH parents not germinating, common garden data were collected from progeny of 8 (out of 11) SH parents and all 6 W parents.

Soil was collected from locations near, but not within the SH1 and W1 populations. This limited the possibility of contamination with seed from population seed banks. In order to identify whether contamination occurred despite our efforts, seeds were planted in an X-shaped pattern in each pot. Soil was collected within a week of seed potting to minimize biotic changes in the soil that might occur as a result of storage method. Neither SERP soil nor SERP seed was used in the common garden experiment because of the lack of differentiation of this population from the W1 population in the 1998 results.

A reciprocal planting design allowed for seed from each population to be planted in its own and the other's soil (Table 1). Each pot was labeled with a unique 3-digit randomly generated number to prevent bias when measuring plant characters. Recorded measurements were matched to the plant parent population only at the completion of the experiment.

A wick-based watering system was used, where the pots were placed on moist quilt batting dipped in tap water. This kept the flow of water to the base of the pots consistent, and pots were able to take up as much water as was transpired or evaporated. No extra fertilization was used. The pots were placed on the rooftop of Duncan Hall at SJSU for the months of February through April. In late April, the rooftop was so hot and sunny that the watering system was unable to keep up with the plants' water needs without daily attention. The pots were moved to a northwest-facing patio in Pacifica for the remainder of the experiment.

Germination and leaf color were monitored on a weekly basis. Pots were thinned to one plant per pot by retaining the plant growing closest to the center of the pot. In cases where several plants were
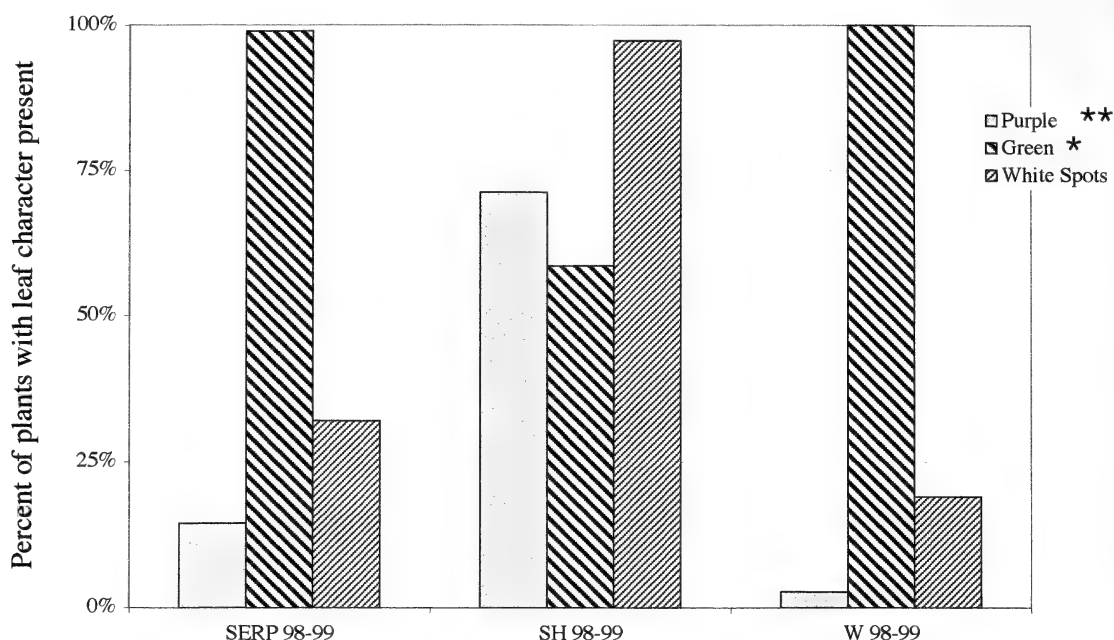
Fig. 1.   Percent presence of leaf characters for all populations, 1998 and 1999 combined. *SH populations different from W and SERP populations (P < 0.01). **All 3 soil types different from each other (P < 0.01).

equidistant from the center of the pot, the largest plant was kept. Leaf color data were collected from all the leaves of each plant. When plants flowered, torus rim width data were collected from all flowers.

Data analysis. The majority of statistical tests were performed in SAS (1990 Ver. 6.0) using the general linear model. G-fit tests performed in Microsoft Excel (1998 Ver 7.0) were used to test for differences among populations in frequencies of discrete characters (Sprinthall 1987). Discrete character frequencies were normalized before analysis. The Bonferroni correction was used in deciding the critical value (adjusted from alpha = 0.05) to minimize the risk of coming upon a chance difference between populations because of the number of characters being compared. A repeated measures MANOVA (SYSTAT 1992 Ver. 5.2.1) was used to define differences over time in 1999 data for torus rim width and number of floral units per plant. All percentage data were arcsine transformed prior to analysis.

RESULTS

Field data collection. To show the total variability in expression of leaf color characters in 2 very different climatic years, leaf color data was combined over 1998 and 1999 for analysis. All 3 populations differed from each other in the purple-leaf character. Purple leaves were much more prevalent in SH populations than in either the SERP or W populations (Fig. 1), but the SERP population had significantly higher number of leaves with purple

than the W populations (P < 0.01). All plants at SERP and W sites in both years had leaves with visible green, but many plants at SH sites lacked visible green pigment. Almost all plants at SH sites had white-spotted leaves, but less than a third of plants at the other sites had this leaf coloration character. While SERP and W populations were similar for green-leaf and white-spotted-leaf characters, SH populations were different from both for these characters (P < 0.01). No differences were found in the distribution of the red-tipped leaf character in 1998.

Differences in floral characteristics were found among populations in 1998 (Table 2). The torus rim was much narrower in the SH populations than in the W and SERP populations (P < 0.01). The bicolor flower character was less prevalent in the SH population in 1998 than in the other two populations (P < 0.01). In 1998, SH sites also tended to have more floral units than the other two site types (P < 0.01).

Floral measurements were taken over time in 1999 to test the validity of a single-date sampling scheme in 1998. If the characters changed over time, differences observed in 1998 could be attributed to the date of sampling. No differences were found in torus rim width over time (P = 0.14). There was a statistical interaction between measurement date and population site for the bicolor flower character (P < 0.002, Fig. 2): the number of bicolor flowers increased over time in the SERP population (P < 0.01), but remained about the same in the other two populations, although the dip in
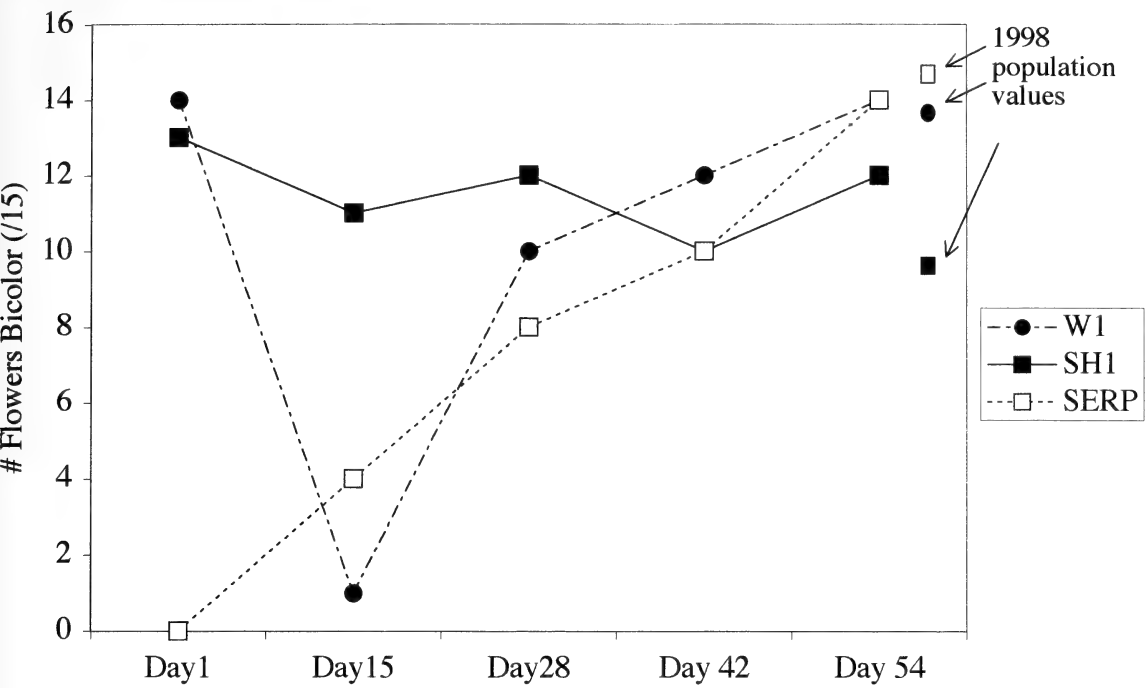
FIG. 2.   Number of bicolor flowers ($n = 15$) for W1, SH1, and SERP populations over time in 1999. Normalized values from 1998 are included. Change over time significantly different among all 3 populations ($P < 0.01$).

the W population in week 2 is not a random effect ($P < 0.01$). The number of floral units per plant increased over time in all populations, but increased more slowly in the SERP population versus the other two populations (Fig. 3).

Since torus rim width did not change over time in 1999, all collection dates and years were lumped to confirm the differences among populations. There was a year by site statistical interaction for this character ($P < 0.0001$). Torus rims were larger in 1999 compared to 1998, but the populations kept their size difference relative to each other: SH rims were the smallest, W rims were the largest, and SERP rims were intermediate (Table 2).

Common garden experiment. No *E. californica* germinated outside the X-shaped seed planting pattern. This does not prove the soil was uncontaminated with an existing seed bank, but such contamination is unlikely. Leaf phenotype remained constant throughout the experiment: once true leaves emerged, they did not change color over time. All SH progeny had purple leaves, regardless of the soil type in which they were grown (Fig. 4). Two W progeny had purple leaves when grown in SH soil, but this distribution was not very different from W in the field. Green leaves were more often absent from SH progeny, again regardless of soil type. All SH progeny had white-spotted leaves, regardless of soil type, where this character was only sometimes present in W progeny.

All plants planted in W soil flowered, regardless

of parent type, but only 7 of the 11 SH plants flowered in their own soil, and only 1 of the 7 W plants flowered in SH soil. Torus rim width (Table 3) is influenced by parent population ($P < 0.001$), individual parent plant ($P < 0.001$), and soil type ($P < 0.0162$): rim width for SH plants was less than for W plants in both soil types, however, torus rims from both parent sources were smaller in SH soil compared to W soil.

DISCUSSION

The differences observed between the populations in terms of the bicolor characteristic and the number of floral units in 1998 were due to the single-date sampling scheme. As shown from the 1999 data, the populations do differ in their expression of these traits, but with the single-date sampling scheme in 1998, lack of difference could just as easily have been observed. This change in some traits over time should serve as a cautionary note to other researchers who plan to sample populations only once per year. The change in flower color and number of floral units over time is not a similarly-expressed trait: the type of change over time varies among populations. It is difficult to say what affects this change over time in some populations but not others. Different types of drying patterns and different soil chemistries at the population sites could be responsible, or these differences could be due to differential responses among the populations to the same environmental factors. Since *E. californica* is
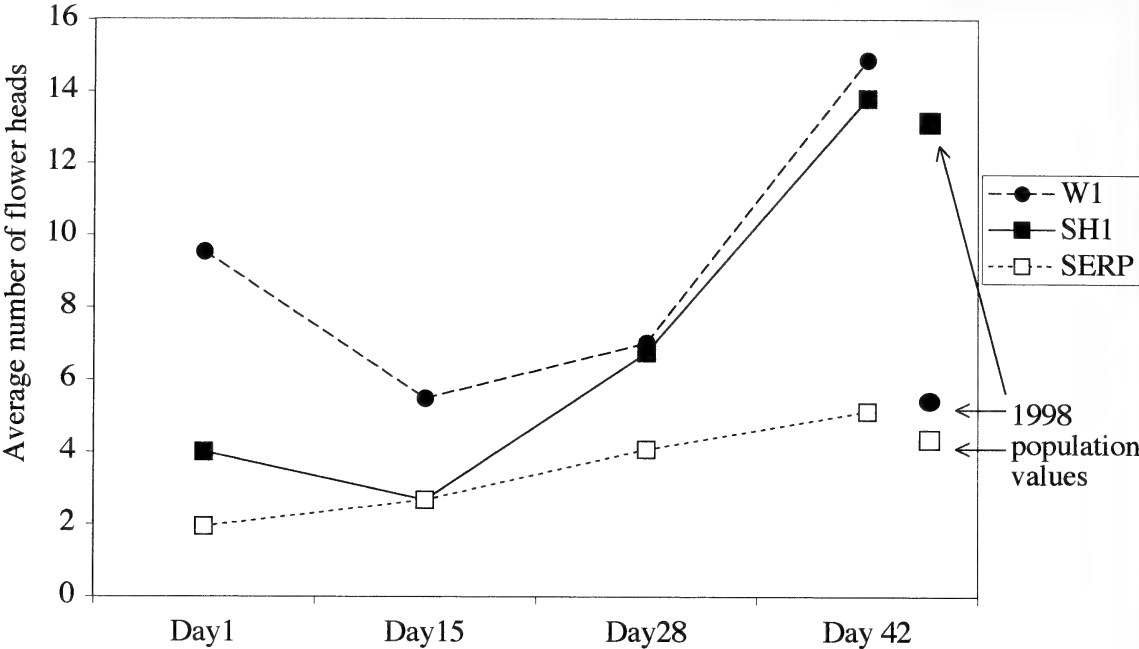
Fig. 3. Average number of flowers per plant for W1, SH1, and SERP populations over time in 1999. Single values from 1998 are included. Change over time significantly different among all 3 populations (P < 0.01).

a plant that has an indeterminate flowering system, the dip seen at Day 15 in number of floral units in W and SH populations is puzzling. We would expect the number of floral units to increase throughout the season. It is possible that a subpopulation of early-flowering plants was sampled at Day 1 and that Day 15 represented the start of the season for a later-flowering subpopulation.

Torus rim width does not appear to change over the flowering season and differences observed between the populations in 1998 were confirmed when the data for the two years were analyzed together. Torus rim width did change between years, and while this indicates some plasticity for this character, it also indicates that the variability is constrained differently within each population.

In the common garden experiment, SH plants kept their purple and white coloration even when planted in Wilder Ranch soil. All SH plants had purple and white coloration even though, while the expression of white coloration is close to 100% in the field, the expression of purple coloration in the field is lower. Progeny from only 8 SH plants were used in the common garden experiment, so it is likely that this difference between common garden and field is due to small sample size. It is clear that the expression of leaf coloration characters that contribute to population differentiation in *E. californica* is phenotypically stable. The purple-leaf, white-spotted characteristic of sand hills plant leaves does not appear to be a direct response to soil type. Although the differences in leaf color are phenotypically stable, they may not be genetic. Effects of the maternal environment in which the seed ripens have been known to include everything from seed germination rates to progeny plants' tolerance to saline environments (see Rossiter 1995 for review). Although leaf color in particular has not been shown to be determined by maternal environment, seed gathered from controlled pollinations of the potted plants should be grown to determine the

Table 2. Floral Characteristics. All averages ± 1 SD. [1] For 1998 and 1999 data combined, both populations from each soil type were included. [a,b,c] For each row, values with different letters are statistically different (P < 0.01).

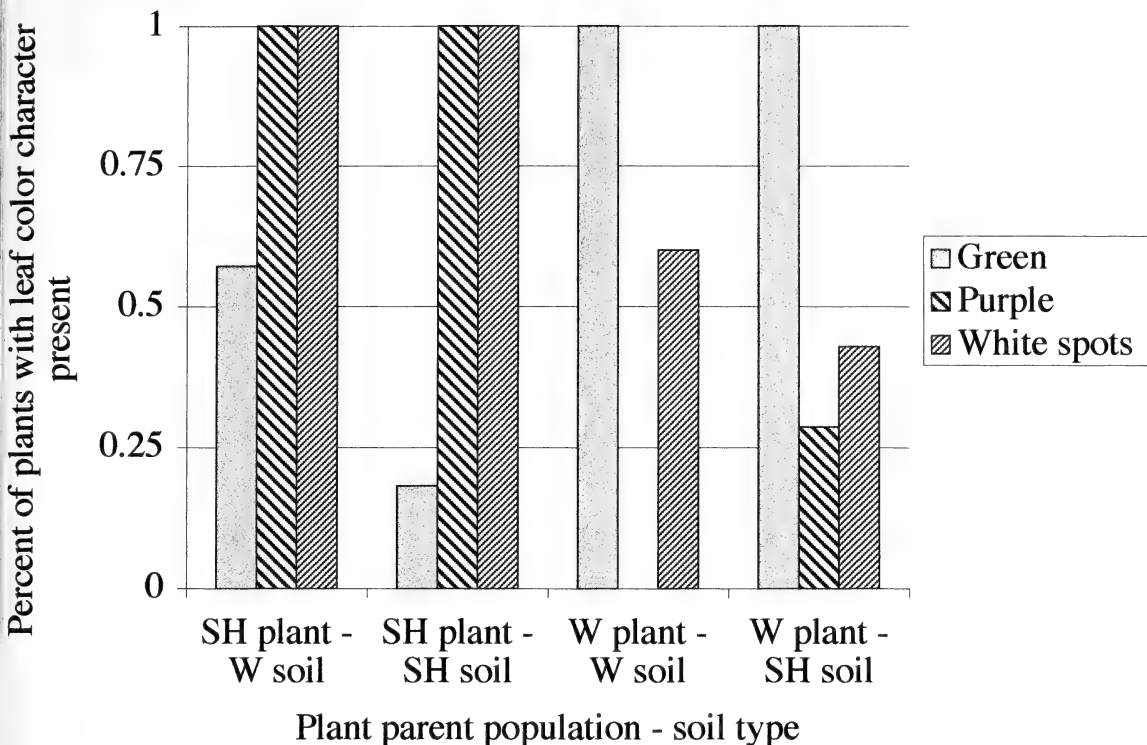|	W[1]	SH[1]	SERP
# floral units 1998	5.90 ± 5.05[a]	12.78 ± 15.9[b]	4.15 ± 3.27[a]
% big color 1998	92.0[a]	65.3[b]	95.5[a]
Torus rim (mm) 1998	1.42 ± 0.7[a]	1.04 ± 0.2[b]	1.41 ± 0.06[a]
1998 and 1999 combined	2.34 ± 1.04[a]	1.14 ± 0.47[b]	1.52 ± 0.62[c]
1998	n = 50	n = 49	n = 66
1998 and 1998	n = 141	n = 142	n = 143

FIG. 4.   Leaf color characteristics in the common garden experiment.

strength of any effects of maternal environment upon leaf phenotype.

Population differentiation is a relatively common phenomenon, but differentiation among populations is expected to be less strong when the flowers are large and the plants outcross than when the flowers are small and the plants are autogamous (Linhart and Grant 1996). Floral characteristics are less likely to be divergent among populations than vegetative ones (Slentz et al. 1999), as usually even the most disparate populations still have the same pollinator species, and thus floral characters tend to be uniformly selected. On the other hand, the characters measured in this study may not be undergoing selection at all.

While a few leaves with purple coloration and white spots were found at W and SERP locations, no plants at these locations had the vibrant purple

coloration masking the visibility of green pigments in their leaves. The sand hills are host to many endemic species (Lee 1996), probably adapted to the particular edaphic environment. The phenotypic stability of leaf-color differences and the influence of parent population on torus rim width indicate that the sand hills population is probably genetically differentiated from the other two populations in this study. Proximate causes of this differentiation are still a mystery: is this differentiation maintained by lack of gene flow into the population, or solely by strong selective forces at the population site?

Even though *E. californica* is a near-obligate outbreeder, pollinated by insects and wind which can carry pollen over a considerable range, Cook (1961) found that *E. californica* populations can be differentiated in as small a scale as hundreds of feet. Differentiation has also been found at distances of less than 3 km (Clark and Charest 1992). The balance between phenotypic plasticity and differential adaptation is not known in this species. Both Cook's and Clark and Charest's results were from field observations: only self-compatibility was tested in a common garden experiment by Cook. It is certainly possible that the species is not as plastic as once thought (i.e., the same genes reacting differently to different environments), but instead adapts locally (different genes in different environments) to exhibit the great variety we observe. A

TABLE 3.   TORUS RIM WIDTH IN COMMON GARDEN EXPERIMENT BY PARENT POPULATION AND SOIL TYPE. All averages ± 1 SD.

Parent population	Soil type	Torus rim width (mm)	Total
SH	W	1.07 ± 0.53	7
SH	SH	0.54 ± 0.48	7
W	W	2.91 ± 0.79	5
W	SH	2.00	1

confounding factor to further investigation of local adaptation is the widespread use of *E. californica* cultivars in landscaping and the success of the species at colonization. Future studies may wish to attempt to determine the extent of cultivar introgression for older populations (Clark and Charest 1992).

This study was designed to determine if the populations at the sand hills at the very least represent an ecotype of the *E. californica* species (*sensu* Toresson 1922 and Kruckeberg 1951). A sand hills ecotype may be indicated by these results. Testing the interfertility of sand hills with surrounding populations and examining the possibility and efficacy of gene flow to the sand hills population will give more information on how the leaf coloration of the *E. californica* at the sand hills is maintained.

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GEOGRAPHIC VARIATION IN THE FREQUENCIES OF TRICHOME PHENOTYPES OF *DATURA WRIGHTII* AND CORRELATION WITH ANNUAL WATER DEFICIT

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Abstract

The perennial plant species, *Datura wrightii* Regel (Solanaceae) is dimorphic for leaf trichome type. Some plants produce almost exclusively short, non-glandular trichomes, while other plants within the same population produce almost exclusively longer, glandular trichomes. In a previous survey of 19 southern California populations, the frequency of plants producing glandular trichomes ranged from 0–82%, and plants with glandular trichomes were absent from desert populations. Here we expand our studies to a total of 56 *D. wrightii* populations from central and southern California. We also examined the relationship between the frequency of glandular trichomes and two factors that broadly determine the availability of water at each site. The first was mean annual rainfall, while the second was mean annual evapotranspiration rate. The frequency of plants with glandular trichomes increased with increasing mean rainfall and decreased with increasing mean annual evapotranspiration rate. Combined, these two environmental variables accounted for about one-third of the variation in the proportion of plants with glandular trichomes. Results suggest that the production of a water-based exudate by plants with glandular trichomes may impose an additional demand for water on those plants compared to plants with non-glandular trichomes. Because of this additional water demand, the frequency of plants with glandular trichomes may decline relative to that of plants with non-glandular trichomes as available water becomes more limiting.

Introduction

Trichomes, or plant hairs, are found on aerial parts of plants in a multitude of forms. This diverse group of structures can be arbitrarily subdivided into glandular, secretory trichomes and non-glandular trichomes (Levin 1973). Among the suggested ecological functions of trichomes are maintenance of the water balance in the leaves, deflection of intense solar radiation, and protection against herbivores (Levin 1973; Ehleringer 1984; Duffey 1986). Both glandular and non-glandular trichomes have been described in several genera within the Solanaceae (Luckwill 1943; Lemke and Mutschler 1984; Gregory et al. 1986; Ogundipe 1992).

Individual plants of *Datura wrightii* Regel (Solanaceae) produce mostly (>95%) glandular trichomes or mostly (>95%) non-glandular trichomes (van Dam et al. 1999). Plants that produce glandular trichomes feel sticky when touched, while plants with non-glandular trichomes feel velvety. The difference in trichome morphology is under the control of a single Mendelian gene, with the glandular condition dominant to the non-glandular condition (van Dam et al. 1999). Hereafter, we refer to plants with non-glandular trichomes as sticky plants and plants with glandular trichomes as velvety plants. Sticky plants produce an exudate composed of acyl sugar esters in water, while velvety plants do not (van Dam and Hare 1998a). These plant types grow adjacently in populations in which they co-occur, often with their branches interdigitated, indicating that microsite specialization of the types is unlikely. The trichome dimorphism is important in determining plant susceptibility to herbivores. Velvety plants are more susceptible to whiteflies and the tobacco hornworm, *Manduca sexta* (Johannson) (van Dam and Hare 1998a), but sticky plants are more susceptible to a mirid bug, *Tupiocoris notatus* (Distant) (van Dam and Hare 1998b; Elle and Hare 2000).

Previously, van Dam et al. (1999) surveyed the distribution of velvety and sticky *D. wrightii* phenotypes in 19 southern California plant populations and found that the frequency of the sticky phenotype varied from 0% to 82%. They suggested that the production of a water-based exudate by glandular trichomes might be especially costly in arid environments, thus possibly accounting for the relative scarcity of sticky plants in the deserts (van Dam et al. 1999). Here, we expand that initial survey to include a total of 56 plant populations not only from southern California, but also from coastal and inland central California as well. We also explore in more detail the potential interaction between water availability and glandular trichome production by analyzing the frequency of sticky plants as a function of overall water availability, as indexed by mean annual rainfall and mean annual evapotranspiration demand.

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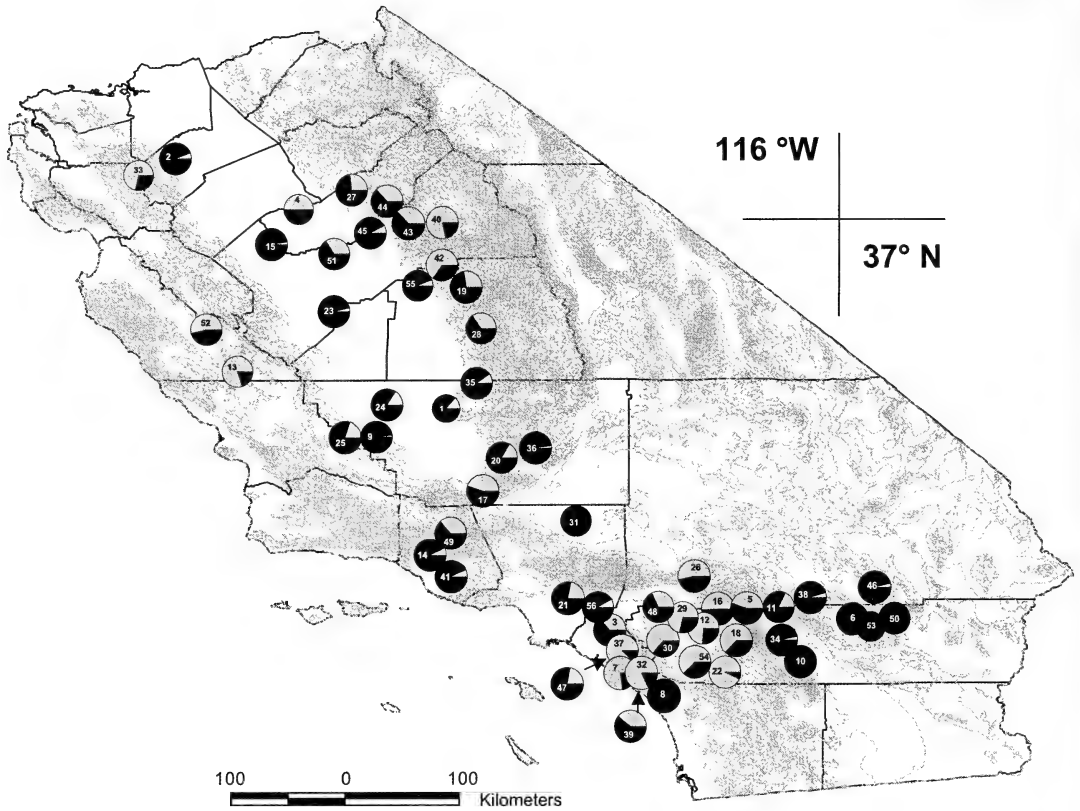
FIG. 1. Sampling locations for sticky and velvety *D. wrightii*. Frequencies of sticky plants are shown in gray, and frequencies of velvety plants are shown in black. The number within each graph refers to numbered populations described in Table 1.

MATERIALS AND METHODS

Datura wrightii is a perennial plant species found in sandy or gravelly dry places in the southwestern U.S. and Mexico (Avery et al. 1959; Munz 1973). Despite the production of large trumpet-shaped flowers, self-pollination predominates, and outcrossing rates are no more than 30% (Snow and Dunford 1961; E. Elle, personal observation).

The phenotype of plants was determined within 56 plant populations of varying size in southern and central California (Fig. 1, Table 1). The phenotype of at least 25 plants in each population was classified by touch and sight into either sticky or velvety categories. The presence or absence of glandular trichomes was confirmed with a hand lens (10×). Most populations were sufficiently small that every individual was examined. The southern California populations were censused in 1997, the San Joaquin Valley and Sierra foothill populations were censused 1998, and the central coast populations were censused in 1999. Sampling was conducted in August or September of each year to ensure that plants were expressing their adult trichome phenotype (van Dam et al. 1999).

Mean annual rainfall at each sampled location was obtained from a map of California annual pre-cipitation published by the National Resources Conservation Services PRISM Climate Mapping Project. This map shows lines of equal mean annual rainfall (isohyets) based upon records taken from 1961 through 1990 plotted at 5 cm. Mean annual rainfall was interpolated between adjacent isohyets to the nearest 2.5 cm. Thus, mean annual rainfall is used as an index of water "supply" to all sampled sites.

An index of mean annual water "demand" that is widely used in irrigation management is "reference evapotranspiration," and is based on the amount of water that would evaporate from an open pan. Values for mean annual reference evapotranspiration (ET_0) were obtained from a map published by the California Irrigation Management Information System (CIMIS) that divides California into 18 evapotranspiration zones.

An index of overall water deficit was calculated for each site by subtracting the mean annual rainfall from the mean annual ET_0 for each site. A value of zero would indicate that mean annual rainfall equaled mean annual ET_0, while positive values would indicate that mean annual ET_0 exceeded mean annual rainfall. The relationship between the percent of plants within populations expressing the

TABLE 1.   LOCATIONS OF *D. WRIGHTII* POPULATIONS SAMPLED FOR THE FREQUENCY OF TRICHOME TYPES. Populations are numbered as in Figure 1. All localities are in California.

1. 155 & 65. Roadside population near the intersection of State Highways 155 and 65, near Mile Marker # 20 on State Highway 155.
2. 33 & 152. Roadside population at the intersection of State Highways 33 and 152 near Dos Palos.
3. Arroyo Trabuco. Natural population within O'Neill Regional County Park, Orange Co.
4. Avenue 22 & Road 191/2. Natural population in an abandoned field bordering this intersection in Madera Co.
5. Banning. Roadside population south of Banning on Old Banning Road.
6. Barker Dam. Natural population, Joshua Tree National Park.
7. Bell Canyon. Natural population, Caspers Regional Wilderness Park, Orange Co.
8. Bonsall. Roadside population along State Highway 76 south of Bonsall.
9. Buttonwillow. Roadside population near the intersection of Elk Grove Road and State Highway 158.
10. Carrizo Canyon. Natural population off of State Highway 74.
11. Casino Morongo. Roadside population near this Indian casino on State Highway 62.
12. Coyote Pass. Natural population within the Lake Perris State Recreation Area.
13. Estrella Road. Roadside population north of the intersection of Estrella Road and State Highway 46.
14. Fillmore. Roadside population near the eastern city limits on State Highway 126.
15. Firebaugh. Roadside population at the intersection of State Highway 33 and Douglas Avenue.
16. Gilman Springs Road. Roadside population south of State Highway 60, approx. 0.8 mi. south on Gilman Springs Road.
17. Gorman. Roadside population on Gorman Road, approximately 2 miles east of Interstate 5.
18. Idyllwild. Natural population off State Highway 243 approximately two miles south of Idyllwild.
19. Kaweah Lake. Natural population at the Lemon Hills Recreation Area on State Highway 198.
20. Kern River Canyon. Roadside population on State Highway 178, near Call Box # 178-128.
21. La Palma. Roadside population at the intersection of La Palma Road and Huxford Avenue at the east end of Yorba Regional Park.
22. Lake Elsinore. Roadside population near the intersection of Riverside Avenue and Collier Road.
23. Lemoore. Roadside population near the intersection of Idaho Street and 19th Avenue.
24. McFarland. Weedlot population on Highway 43 directly west of McFarland in waste ground near an abandoned railroad siding.
25. McKittrick. Weedlot population near the intersection of State Highways 58 and 33.
26. Mill Creek. Natural Population at the Mill Creek Ranger Station, State Highway 38.
27. Millerton Lake. Natural population around the Millerton Historic Courthouse.
28. Milo Ranger Station. Roadside population on Yokohl Road near the Milo Ranger Station.
29. Moreno Valley. Weedlot population near the intersection of Moreno Beach Drive and Ironwood Avenue.
30. Motte. Natural population within the Motte Rimrock UC Reserve along Pictograph Trail.
31. Neenatch. Roadside population on State Highway 138 approximately midway between Pearblossom and Little Rock, 4 mi. east of the California Aqueduct.
32. Ortega Flats. Natural population in Caspers Regional Wilderness Park, Orange Co.
33. Pacheco Pass. Weedlot population off Highway 152 at Dinosaur Point boat launching ramp, San Luis Reservoir.
34. Palm Springs. Weedlot population in the vicinity of the parking lot for the Palm Springs Tram off State Highway 111.
35. Porterville Road. Roadside population north of Glenville, on Jack Ranch Road.
30. Rich Bar. Weedlot population along State Highway 178 near the Rich Bar Overflow parking lot.
37. Riley Wilderness. Natural population within Riley Wilderness Park, Orange Co.
38. Route 62. Roadside population 2 miles east of the boundary of Joshua Tree National Park.
39. San Onofre. Roadside population along Interstate 5.
40. Sequoia National Forest. Roadside population along State Highway 180 approximately 1 mile inside National Forest boundary.
41. Simi Valley. Weedlot population at Los Angeles Avenue and Angus Road.
42. Three Rivers. Natural population in a field on North Fork Road 4.8 miles from State Highway 198.
43. Tollhouse Grade. Roadside population on Tollhouse Road at the Sierra National Forest boundary.
44. Tollhouse Road. Roadside population between Humphrey's Station and Tollhouse.
45. Trimmer Springs Road & Belmont Avenue. Roadside Population at intersection.
46. Twentynine Palms. Roadside population near the intersection of Utah Trail and Underhill Road near the north entrance to Joshua Tree National Park.
47. UC Irvine. Weedlot population in an undeveloped field near University Avenue and Beech Tree Road.
48. UC Riverside. Natural population within the UC Riverside Botanic Gardens grounds.
49. Val Verde. Population in an abandoned field on San Martinez Road off State Highway 126 near Val Verde County Park.
50. White Tank. Natural population within Joshua Tree National Park.
51. Whitesbridge Road. Roadside population on State Route 180 near Mendota.
52. Wild Horse Road. Weedlot population in an abandoned field south of King City, east of U.S. 101.
53. Wilson Canyon Wash. Natural population within Joshua Tree National Park.
54. Winchester Road. Weedlot population on undeveloped ground near the intersection of Winchester Creek Road and State Highway 79.
55. Woodlake. Natural population along a stream on Highway 245 directly east of the Woodlake Airport.
56. Yorba Linda. Weedlot population on a vacant lot near Weir Canyon Road and Savi Ranch Road.

sticky phenotype and mean annual water deficit was determined by linear regression analysis.

RESULTS AND DISCUSSION

The frequency of sticky plants varied from 0% in six populations, mostly from the Mojave Desert, to 93% in a population near Lake Elsinore. Other plant populations having more than 75% sticky individuals included two populations from the coastal mountains of Orange County (Ortega Flats and Riley Wilderness State Park), one from the mountains of the central Coast Range (Estrella Road), and another from the foothills of the central Sierra Nevada range (Sequoia National Forest).

Mean annual precipitation from these sites ranged from a low of 10 cm annually at the Twentynine Palms population in the Mojave Desert to a high of nearly 69 cm annually at the Idyllwild population in the San Jacinto Mountains. Sites where rainfall also averaged 15 cm or less include all of the Mojave Desert populations as well as populations in the southwestern portion of the San Joaquin Valley (McKittrick, Buttonwillow). Other populations where mean annual rainfall was relatively high (50 cm or more) were limited to other areas in the foothills of the Sierra Nevada mountain range (Porterville Road, Milo Ranger Station, Tollhouse Road, Tollhouse Grade, and Sequoia National Forest) or the base of the San Bernardino Mountains (Mill Creek).

Highest mean annual ET_0 (183 cm, Zone 18) occurred in the two populations in the Coachella Valley (Carrizo Canyon, Palm Springs), followed by the three populations in Joshua Tree National Park (Barker Dam, White Tank, Wilson's Creek, 168 cm, Zone 17), and the two populations from the floor of the San Joaquin Valley in Fresno Co. (Whitesbridge Road, Lemoore, 157 cm, Zone 16). Lowest mean annual ET_0 occurred in the San Onofre population (Zone 1, 84 cm), followed by the populations on the coastal plain of Orange and San Diego Counties (UC Irvine, Bonsall), and at the base of the Santa Ana Mountains in Orange County (Arroyo Trabuco, Bell Canyon, Ortega Flats, Riley Wilderness, Zone 4, 118 cm).

Overall, the percentage of sticky plants was positively correlated with increasing mean annual rainfall (r = 0.455, P = 0.004, n = 56) and negatively correlated with increasing mean annual ET_0 (r = −0.474, P = 0.0002, n = 56). Mean annual ET_0 and mean annual rainfall were significantly, but imperfectly negatively correlated (r = −0.32, P = 0.016, n = 56), so that when the two variables were combined into the new variable, "mean annual water deficit," the percentage of sticky plants declined with increasing water deficit, (r = −0.572, P < 0.0001, n = 56), and water deficit accounted for 33% of the variation in the percentage of sticky plants (Fig. 2). These results suggest that sticky plants may be at a selective disadvantage in rela-
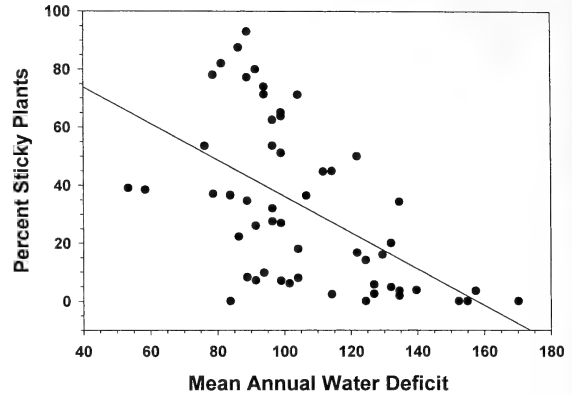

FIG. 2. Percent of sticky plants in each population as a function of water deficit. Water deficit was calculated as the mean annual rainfall at each site subtracted from the mean annual evapotranspiration (ET_0) at each site. Regression equation: Percent sticky = 98.90 − (0.6370 * water deficit); P < 0.0001, n = 56.

tively dry environments because glandular trichomes may impose an additional water demand on sticky plants, as has been found for at least one other plant species (Lauter and Munns 1986).

The low proportion of variance in the frequency of sticky plants that is accounted for by water supply (rainfall) and demand (ET_0) suggests that other factors may also influence the frequency of sticky plants in particular locations, and we know from previous studies that trichome morphology strongly influences the susceptibility of plants to insect attack (van Dam and Hare 1998a, 1998b; Elle et al. 1999; Elle and Hare 2000). Within sites of equivalent water availability, natural selection may favor sticky plants over velvety plants when the herbivore community is dominated by species such as whiteflies, flea beetles, and *M. sexta* and disfavor sticky plants when the herbivore community is dominated by species like *T. notatus* that are particularly well adapted to feed on plants with glandular trichomes (Elle and Hare 2000). Thus, a portion of the remaining variation in trichome frequencies could be accounted for by variation in the structure of herbivore communities attacking plant populations in areas of similar water availability. Such variation in herbivore community structure has already been shown for different populations within southern California habitats (Elle and Hare 2000).

Additionally, because these plant populations also are relatively small, and self-pollination predominates (Snow and Dunford 1961), founder effects and limited gene flow among plant populations may also contribute to variation in phenotype frequencies among plant populations with similar water availability. In order to completely account for all of the variation in trichome frequencies among these plant populations, it would be necessary to consider the actual site-specific water avail-

ability, the pattern and magnitude of damage by insect species differentially adapted to trichome type, and the ability of plant populations to respond genetically to natural selection by these factors. Nevertheless, the data presented here suggest that variation in the availability of water, as indexed by variation in mean annual rainfall and mean annual evapotranspiration, may provide a broad gradient of resource availability upon which more specific interactions between *D. wrightii* trichome types and both biotic and abiotic components of the plant's local environments are displayed.

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A NEW SECTION IN THE GOLDFIELD GENUS *LASTHENIA* (COMPOSITAE: HELIANTHEAE SENSU LATO)

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Abstract

Lasthenia Cass. sect. *Ornduffia* R. Chan is a new section in the goldfield genus *Lasthenia* (Compositae: Heliantheae sensu lato).

The goldfield genus *Lasthenia* Cass. (*sensu* Ornduff 1966, 1971, 1993) comprises 20 species and subspecies in six sections. Five of Ornduff's (1966) six sectional circumscriptions are monophyletic based on results from a recent molecular phylogenetic study using nuclear and chloroplast DNA sequences (Chan 2000, Chan et al. in press): *L.* sect. *Baeria* (Fisch. & Mey.) Ornduff, *L.* sect. *Burrielia* (DC.) Ornduff, *L.* sect. *Hologymne* (Bartling) A. Gray in Torr. and A. Gray, *L.* sect. *Lasthenia,* and *L.* sect. *Platycarpha* (Hall) Ornduff. Based on the same data, *L.* sect. *Ptilomeris* (Nutt.) Ornduff (*sensu* Ornduff 1966), which comprises six species [*L. burkei* (Greene) Greene, *L. conjugens* Greene, *L. coronaria* (Nutt.) Ornduff, *L. fremontii* (Torr. ex A. Gray) Greene, *L. maritima* (A. Gray) M. Vasey, and *L. minor* (DC.) Ornduff], is strongly resolved as two well-supported monophyletic groups. *Lasthenia burkei, L. conjugens,* and *L. fremontii* form an unresolved monophyletic lineage; *L. coronaria, L. maritima,* and *L. minor* form another monophyletic group. The relationship between these two groups of species is unresolved. Disparity among these species in chromosome numbers, flavonoid chemistry (Bohm et al. 1974; Ornduff et al. 1974), and morphological features further challenge the monophyly of *L.* sect. *Ptilomeris.* A review of all available data support the separation of *L.* sect. *Ptilomeris* into two monophyletic sections.

The two groups of species can be distinguished by fruit sizes, chromosome numbers, habitat preferences, and, to some extent, by geographic distribution. *Lasthenia burkei, L. conjugens,* and *L. fremontii* have cypselae that are less than 1.5 mm long, have chromosome numbers of $2n = 12$, and are commonly associated with vernal pools. They have distributions mostly limited to interior California. Both *L. burkei* and *L. conjugens* are listed as endangered species in the federal list of endangered and threatened wildlife and plants (Tibor 2001). *Lasthenia coronaria, L. maritima,* and *L. minor* have cypselae more than 1.5 mm long, have chromosome numbers of $2n = 8$ or 10, and are not usually associated with vernal pools although L. minor has been found in vernal pools (D. Keil pers.

comm.). They have wide distributions that include coastal habitats in California (and, for *L. coronaria* and *L. maritima,* elsewhere along the Pacific coast of North America).

Based on phylogenetic results, I propose that the members of *L.* sect. *Ptilomeris* sensu Ornduff (1966, 1993) be relegated to two sections: *L.* sect. *Ptilomeris* sensu stricto with *L. coronaria, L. maritima,* and *L. minor* and *L.* sect. *Ornduffia* with *L. burkei, L. conjugens,* and *L. fremontii.*

Lasthenia Cass. sect. *Ptilomeris* (Nutt.) Ornduff, emend. R. Chan

Plants not associated with vernal pools, leaves entire, irregularly lobed, or pinnatifid, involucres hemispheric to obconic, phyllaries free, receptacles conic, corollas of disc florets 5-lobed, floral pigments remaining yellow in dilute alkali, tips of anthers ovate to obovate, cypselae greater than 1.5 mm long, pappose or epappose, scales of pappi erose, lance-aristate, and/or subulate-aristate, $2n = 8, 10$.

A new section is erected for *L. burkei, L. conjugens,* and *L. fremontii,* and is named for Professor Emeritus Robert Ornduff, in recognition of his outstanding contributions to the understanding of the evolution of *Lasthenia* and other groups in the California flora.

Lasthenia Cass. sect. *Ornduffia* R. Chan, *sect. nov.*
Type species: *Dichaeta fremontii* Torr. ex A. Gray ≡ *Lasthenia fremontii* (Torr. and A. Gray) Greene

Plantae in consortio lacunarum vernalium et foliis plerumque pinnatifidis, involucris hemisphaericis vel obconicis, phyllariis libris (ex parte connatis in una specie), receptaculis conicis vel tholiformibus, corollis flosculorum discorum 5-lobatis, pigmentis floralibus remanentibus flavis in solutionibus dilutis alcalinis, apicibus antherarum linearibus vel anguste ovatis, cypselis <1.5 mm longis, papposis vel epapposis, squamellis papparum erosis vel subulatis-aristatis, $2n = 12$.

Plants associated with vernal pools, leaves usually pinnatifid, involucres hemispheric or obconic, phyllaries free (partly fused in *L. conjugens*), receptacles conic or dome-shaped, corollas of disc florets 5-lobed, floral pigments remaining yellow in dilute alkali solution, tips of anthers linear to narrowly ovate, cypselae less than 1.5 mm long, pappose or epappose, scales of the pappi erose or subulate-aristate, $2n = 12$.

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CORALLORHIZA MACULATA VAR. *OZETTENSIS* (ORCHIDACEAE), A NEW CORAL-ROOT FROM COASTAL WASHINGTON

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Abstract

Corallorhiza maculata var. *ozettensis* is a newly described mycoheterotrophic orchid from western Washington. It occurs in foggy rainforests bordering the Pacific coast of the north Olympic Peninsula. Unlike typical *C. maculata,* its flowers are consistently non-spotted, with a narrow, white labellum bearing two apical undulations and low, non-rugose basal lamellae. Stem cross sections show epidermal cells mostly tangentially elongate, each bearing 4–10 delicate cuticular ridges bounded laterally by narrow sinuses.

In June 1967, I collected a unique, white-lipped *Corallorhiza* near the Ozette Indian Reservation of coastal Washington. Subsequent collections and observations revealed that populations of this coral-root, referred eventually to *C. maculata* (Raf.) Raf. (Buckingham and Tisch 1979), extended northward and inland at least 27 km and 1.5 km, respectively. The type collections are remarkably uniform in color, morphology, cell anatomy, and ecological fidelity, and in this locality occur to the apparent exclusion of contrasting varieties of *C. maculata.* While these plants exhibit homogeneity suggestive of reproductive isolation and are not distributed randomly within populations of spotted *C. maculata,* as are many of its recognized color forms, their structural parameters lie within the limits established for *C. maculata* (Luer 1975, Freudenstein 1997), and I have relegated them to varietal status under that species.

Corallorhiza maculata (Raf.) Raf. var. **ozettensis** E. Tisch, var. nov. (Fig. 1 in part)—TYPE: USA, Washington, Clallam Co., forested bluffs above Cape Alava, 48°10′N 124°44′W, T31N R16W sect. 26, ca. 100′ (30 m) elev., 28 June 1967, *E.L. Tisch 689A & 689B* (holotype, UC; isotype, OSC).

Caulis erectus, 20–60 cm altus, pallidus, roseus-violescens vel brunneo-violescens. Inflorescentia 3–20-flora, 5–17 cm longa, 2–3 cm lata. Pedicelli 1–2 mm longi, erecti vel penduli, bracteati. Bractae ovatae vel lanceolatae, 0.5–1.5(1.8) mm longae, acutae, obtusae, truncatae vel emarginatae. Flores 1.0–1.5 cm longi, 6–12 mm lati; sepala superior oblongo-oblanceolata, obtusa vel emarginata, (6.2)7.0–9.5(9.8) mm longa, (2.0)2.2–2.3(2.5) mm lata, apex purpureus, basis flavus; sepala laterala oblongo-oblanceolata, obtusa vel acuta, (5.8)6.5–9.0(9.4) mm longa, (1.8)2.2–2.3(2.5) mm lata, apex purpureus, basis flavus; petala oblongo-lanceolata, obtusa vel acuta, (5.5)6.0–7.0(7.3) mm longa, (1.7)1.9–2.1(2.3) mm lata, flava; labellum oblanceolatum vel obovatum, trialobatum, trinerviatum, album immaculatum, obtusum, (5.0)5.5–7.5(8.0) mm longum, (2.6)3.1–3.5(3.6) mm latum, apex bi-undulatum; mentum 1.0–2.0 mm longum, 0.4–1.0 mm altum; columna arcuata, 3.5–4.8 mm longa; stigma ca. 0.9–1.3 mm lata. Fructus elliptico-oblongus, purpureus vel brunneus, pendulus, pauci-verrucosus, 1.0–1.5 cm longus, 3–4 mm crassus.

Stems erect, 20–60 cm tall, pale pinkish violet or brownish violet. Racemes 3–20-flowered, 5–17 cm long, 2–3 cm wide. Pedicels 1–2 mm long, erect at anthesis to pendent in fruit. Floral bracts ovate to lanceolate, 0.5–1.5(1.8) mm long, acute, obtuse, truncate, emarginate, or bluntly tridentate. Flowers ascending at anthesis, 1.0–1.5 cm in length, 6–12 mm wide; dorsal sepal forward facing, oblong-oblanceolate, obtuse to obliquely emarginate, (6.2)7.0–9.5(9.8) mm long, (2.0)2.2–2.3(2.5) mm wide, the apex purplish, often with translucent margins, basal portions yellowish; lateral sepals usually spreading, oblong-oblanceolate, obtuse to nearly acute, (5.8)6.5–9.0(9.4) mm long, (1.8)2.2–2.3(2.5) mm wide, the apex purplish, basal portions yellowish; petals forward facing, oblong-oblanceolate, obtuse to acute, (5.5)6.0–7.0(7.3) mm long, (1.7)1.9–2.1(2.3) mm wide, yellowish; labellum oblanceolate or obovate, 3-lobed, nearly always 3-nerved, pure white at early anthesis (darkening with age), obtuse, (5.0)5.5–7.5(8.0) mm long, (2.6)3.1–3.5(3.6) mm wide at the widest part of the median lobe, the apex slightly dilated but rarely crenate-undulate or involute, usually bi-undulate at the tip (Fig. 1), the basal lamellae 1.7–2.2 mm long, arising within 2 mm of the labial attachment and extending to within 2.2–2.5 mm of its apex, non-rugose; mentum yellowish, 1.0–2.0 mm long, 0.4–1.0 mm high, yellow; column yellowish, often arcuate-ascending, 3.5–4.8 mm long; stigma ca. 0.9–1.3 mm wide. Capsule ellipsoidal, purplish to brown, slightly warty, 1.0–1.5 cm long, 3–4 mm thick.

Paratypes. USA, Washington, Clallam Co.: coastal forests at Cape Flattery, 48°23′N 124°44′W, T33N R16W sect. 1, ca. 75′ (23 m) elev., 23 July 1984, *E.L. Tisch 2653* (WTU), *2654* (ORE), *2655*
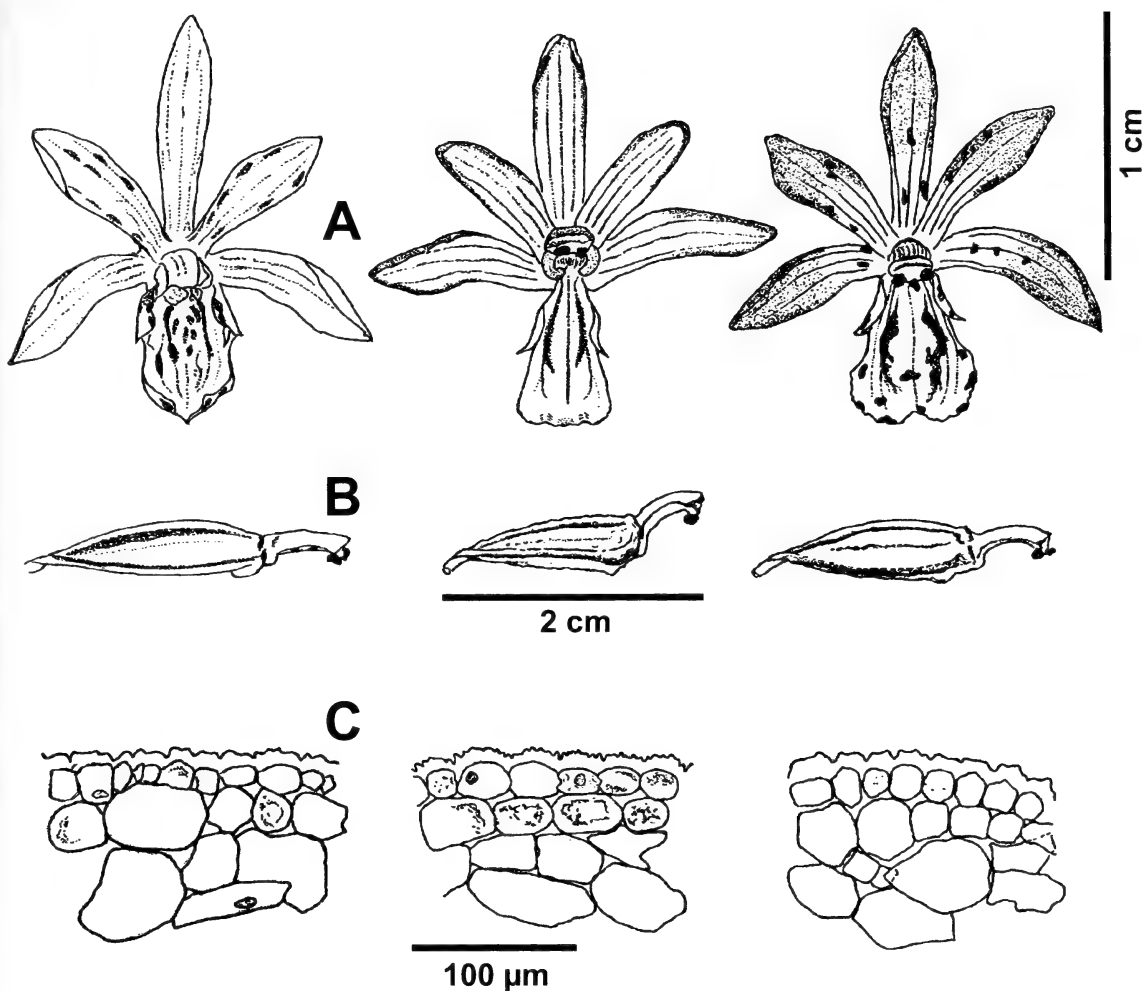
maculata   **ozettensis**   **occidentalis**

FIG. 1.   Illustrations comparing three varieties of *C. maculata*. A. Anterior views taken of living flowers with perianths folded back. B. Lateral views of immature capsules (perianths removed) showing frequent column orientations. C. Portions of stem cross sections taken 1 cm below the inflorescence. Illustrations by Karen Lull-Butler.

(WS); shady coastal forest, ca. 90 m inland, Cape Flattery, ca. 100′ (30 m) elev., 27 July 1984, *E.L. Tisch 2688* (UC), *2689* (OSC); forested bluffs, Portage Head, 48°17′N 124°41′W, T32N R15W sect. 7, ca. 80′ (25 m) elev., 18 June 1988, *E.L. Tisch 3256* (MO), *3257* (V).

Distribution, habitat, and phenology. Corallorhiza maculata var. *ozettensis* grows in moist, foggy, very shady to moderately illuminated forests bordering the northwestern coastline of the Olympic Peninsula. The collection sites, all within 300 m of the Pacific Ocean, are overstoried by mixtures of *Picea sitchensis* (Bong.) Carr., *Thuja plicata* D. Don, *Tsuga heterophylla* (Raf.) Sarg., and *Alnus rubra* Bong. A sparse understory of *Malus fusca* (Raf.) Schneid. and *Rhamnus purshiana* DC. is of-

ten present, while the medium-shrub layer includes *Vaccinium alaskense* Howell, *V. ovatum* Pursh, *V. parvifolium* Smith, and *Menziesia ferruginea* Smith.

The common herb associates are *Blechnum spicant* (L.) Smith, *Polystichum munitum* (Kaulf.) Presl, *Maianthemum dilatatum* (Alph. Wood) Nelson and J. F. Macbr., *Tiarella trifoliata* L., *Listera caurina* Piper, and *L. cordata* (L.) R. Br. In its typical habitats *C. maculata* var. *ozettensis* is inconspicuous and rare. It is mycoheterotrophic and has knobby rhizomes embedded 1–2 dm in moist humus. Depending on weather conditions, it blooms from about mid-June through late July. This is considered "late" flowering for *Corallorhiza* as described by Freudenstein and Doyle (1994) and Freudenstein (1997).

Taxonomic relationships. Luer (1975) called *C. maculata* the most common and variable coral-root in the conterminous United States, and suggested that its color forms, while sometimes clustering in communities, tend to lack morphological identity separate from that of associated spotted individuals. He did not clearly differentiate between forms and varieties. Kartez (1994) synonymized all of the *C. maculata* variants under that single specific epithet. After years of research, Freudenstein (1986, 1992, 1997) narrowed the *C. maculata* complex, north of Mexico, to two intergradient varieties: *maculata* and *occidentalis* (Lindl.) Ames. Brown (1998), however, in his orchid checklist, recognized 8 infraspecific segregates, including forms, within that same complex. The var. *maculata,* a narrow-lipped, late-blooming variant, appears to be uncommon on the Olympic Peninsula, and is often intergradient here with the broad-lipped, early-blooming var. *occidentalis,* which is larger and quite conspicuous, flowering as early as May 5 in the Olympic lowlands. Variety *ozettensis* has a narrow, white labellum bearing two closely adjacent, upward undulations, one to either side of the mid-apex, and low, non-rugose basal lamellae. The labellum tapers to its attachment which is usually less than 1 mm wide. Its lateral and apical margins are semi-entire, contrasting with the crenate-undulate margins of the other two varieties. The narrow cuticular ridges on the stem epidermis number 4–10 per cell, nearly twice as many as the low, rounded ridges bordering comparable cells of vars. *maculata* and *occidentalis* (Fig. 1C). Also, the cauline epidermal cells of var. *ozettensis,* seen in cross sections taken 1 cm below the inflorescence, are >65% tangentially elongate, while those from the two spotted varieties of this region have <50% positioned in that plane. These diagnostic microscopic features were encountered consistently in living stems from 10 specimens of var. *ozettensis,* 15 of var. *occidentalis,* and 7 of var. *maculata.* The latter two varieties, at least on the Olympic Peninsula, have columns that often align with the floral axis, while those of var. *ozettensis* tend to ascend at angles >25° (Fig. 1B), but these tendencies are not entirely reliable.

Superficially, var. *ozettensis appears* to be closely allied with forma *immaculata* (Peck) Howell, a white-lipped variant described from Linn Co., Oregon (Peck 1954), and currently referred to var. *occidentalis* in Brown's (1998) checklist. Actually, this form of *C. maculata* is readily separable from var. *ozettensis.* The *immaculata* holotype (OSC!) has spreading perianth parts, and a crenulate, distally expanded labellum with multiple levels of venation. The latter half of the following key is modeled after Freudenstein's (1997) key to the varieties of *C. maculata.*

KEY TO THREE VARIETIES OF *CORALLORHIZA MACULATA* AS REPRESENTED IN COASTAL WASHINGTON

1. Labellum white at early anthesis (darkening with age), its lateral nerves usually simple; the margins of its central lobe sub-entire . . . .
. . . . *C. maculata* var. *ozettensis*
1. Labellum usually white, spotted with purple, its lateral nerves often prominently branched; the central lobe distally crenate-undulate 2
2. Central lobe of labellum distinctly expanded, its broadest distal portion > 1.5 times wider than its base; labial apex broadly rounded to retuse . . . . . .
. . . . *C. maculata* var. *occidentalis*
2. Central lobe of labellum slightly if at all expanded, its broadest distal portion < 1.5 times wider than its base; labial apex narrowly rounded to acute . . .
. . . . *C. maculata* var. *maculata*

The Ozette coral-root is named after the Ozette band of Makah Indians that occupied the original collection site for hundreds of years.

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NOTEWORTHY COLLECTIONS

NEVADA

ABIES CONCOLOR (Gordon & Glendinning) Hildebrand var. *concolor* (PINACEAE).—Nye Co., Belted Range, Nellis Air Force Bombing and Gunnery Range (NAFBGR), UTM Zone 11 579411E 4143156N (NAD 27), on steep NW slope ca. 1 km south of Indian Spring, 2287 m (7503′), 18 May 1996, *F. Smith and D. Pritchett 3970* (RENO, UNLV, UTC); Nye Co., Belted Range, NAFBGR, UTM Zone 11 582031E 4150875N (NAD27), on steep N slope ca. 5.8 km north of Wheelbarrow Peak, 2417 m (7930′), 15 September 1996, *F. Smith, D. Pritchett and E. Watkins 3982* (RENO, UNLV, UTC); Nye Co., Belted Range, NAFBGR, UTM Zone 11 581185E 4145466N (NAD27), northwest slope of Wheelbarrow Peak ca. 0.5 km from summit, 2349 m (7707′), 28 September 1996 *F. Smith and D. Pritchett 3984* (RENO, UNLV). Specimens were examined by Ronald M. Lanner, Utah State University, Logan, Utah. Forms woodlands with *Pinus monophylla* generally above 2286 m (7500′) on summits and ridges of the central portion (i.e., UTM Zone 11 ~ Northing 4151000 to ~ Northing 4138000) of the Belted Range, especially on N/NW slopes. Characteristic understory spp. include *Chrysothamnus viscidiflorus, Ribes cereum, Artemisia tridentata* and *Poa fendleriana.*

Previous knowledge. Abies concolor var. *concolor* (Rocky Mountain white fir) occurs in Idaho, Utah, Colorado, Arizona, New Mexico, Nevada, and southeastern California while *A. concolor* var. *lowiana* (Gordon) Lemmon (California white fir) is found in California, Oregon, and western Nevada. The nearest known occurrence of *A. concolor* var. *concolor* is on the summit of Bald Mountain in the Groom Range, about 32 km to the east (D.A. Charlet, 1996, Atlas of Nevada conifers, University of Nevada Press, Reno, NV). The nearest known occurrence of *A. concolor* var. *lowiana* is in the southern Sierra Nevada in California, about 250 km due west (R.M. Lanner, 1999, Conifers of California, Cachuma Press, Los Olivos, CA).

Significance. This is the westernmost known occurrence of *Abies concolor* var. *concolor* in Nevada and may also be the westernmost occurrence in the Great Basin (D.A. Charlet, 1996, Atlas of Nevada conifers, University of Nevada Press, Reno, NV).

A large portion (3.1 million acres) of central-southern Nevada is occupied by the Nellis Air Force Bombing and Gunnery Range and has been closed to the public since 1940. Janice Beatley, one of the few botanists who had access to the area, reported *Abies concolor* to be absent from Wheelbarrow Peak (Belted Range) and high peaks elsewhere in the region (J. Beatley, 1976, Vascular plants of the Nevada test site and central-southern Nevada: ecologic and geographic distributions, U.S. Department of Commerce, National Technical Information Service). Beatley must have approached Wheelbarrow Peak from the southeast (probably from the road to Johnnies Water); we approached from the northwest where *Abies concolor* is abundant. The fact that extensive stands of a species of this size were only documented for the first time in 1997 (T. Knight, F. Smith, and D. Pritchett, 1997, An inventory for rare, threatened, endangered and endemic plants and unique communities on Nellis Air Force Bombing and Gunnery Range, Clark, Lincoln and Nye Counties, Nevada, The Nature Conservancy of Nevada, Las Vegas) is an indication of how little botanical inventory work has been done in the Belted Range and suggests that further such work will prove fruitful. Work was supported by funds from the Department of Defense's Legacy Resource Management Program awarded to The Nature Conservancy of Nevada. We are grateful to Cols. Thomas Lillie and Douglas Ripley for support and review of manuscripts.

—DANIEL PRITCHETT, University of California White Mountain Research Station, 3000 E. Line St., Bishop, California, 93514; FRANK J. SMITH, Western Ecological Services, Inc., P.O. Box 422, Millville, UT 84326; TERI KNIGHT, Director of Science and Stewardship, Nevada Field Office, The Nature Conservancy, 1771 E. Flamingo #B111, Las Vegas, NV 89119.

REVIEWS

Savannas, barrens and rock outcrop plant communities of North America. Edited by Roger C. Anderson, James S. Fralish, and Jerry M. Baskin. 1999. Cambridge University Press, Cambridge UK. 470 p. Hardcover $110.00. ISBN 0-521-57322-X.

This book synthesizes information on a number of North American plant community types found in environments that restrict tree and other plant growth due to harsh substrata and or other factors. Why combine savannas with edaphic complexes? I did not find a satisfactory answer to this. I think there is sufficient logic, and material, especially since some additional community types could have been included, for two somewhat smaller books. This would have better served readers who want a less expensive book on either topic, but not both.

Despite this opinion and some other criticisms, I found much to like about this book. It is divided into 26 chapters, each describing an individual community, or in some cases a broad vegetation type (e.g., Southeastern Pine Savannas, Ponderosa Pine and Subarctic Woodlands). Forty-seven leading experts on the subjects selected contribute to create an authoritative treatment. There are three indexes; plant, animal, and topic. The chapters on strongly edaphic or extreme-soil-condition communities comprise the portion of the book that is the most valuable in terms of types that have not previously received enough attention. While information on, for example, Serpentine barrens of Western North America, is readily available (e.g., Kruckeberg's book), it is not for communities such as mid-Appalachian Shale Barrens, Granite Outcrops of the Southeastern United States or Southern Ontario, and especially Niagra Escarpment, Great Lake Alvar (limestone/marble substrata), and Sand Shinnery Oak communities. There is no mention of these in my 1988 edition of *North American Terrestrial Vegetation,* and the authors of the chapter on Sand Shinnery Oak (S. S. Dhillion and M.H. Mills) mention that theirs is the first ever review of the ecology and future conservation of this surprisingly (at least it was to me) extensive community.

To get a sense of how thoroughly community types are treated, note that *North American Terrestrial Vegetation* has seven pages on which Serpentine is mentioned compared to 2 chapters and 29 pages on the topic in this more specialized book. Thus, the book contains much enlightening information, even for ecologists with an encyclopedic level of knowledge of North American vegetation.

Savannas and relatively widespread vegetation types discussed in this book are treated in reviews elsewhere, but not typically with as great an emphasis on conservation and management issues, nor

the effort to integrate plant and animal ecology found throughout this text. Unfortunately, savanna is a nebulous term. As a result there are chapters on vegetation often thought of as woodland (i.e., Pinyon-Juniper) that some might not expect to find. In fact, three chapters use woodland rather than savanna in their title (e.g., Subarctic). Conversely, some savanna or woodland types are left out (e.g., Garry Oak, sub-tropical). There are some edaphic complexes omitted as well, such as, in Western North America, Sierran granite outcrops, and scabland associated with lava flows in the Cascades and on the Modoc Plateau, etc. However, these subjects have been studied relatively little by ecologists and others, there may be insufficient literature from which to prepare a review.

There is not a consistent set of topics covered in each chapter, which is partly understandable considering how different some of the chapter subjects are. For example, while fire is a keystone process maintaining the open tree spacing in many savanna communities, fire effects in rock outcrop and some barrens communities are nil. Nonetheless, there could be greater consistency among chapters. While most authors provided useful, concise summaries, they are missing from 6 chapters. In addition, the use and effectiveness of maps and photos is variable. Some chapters lacked sections on conservation and management despite these being important overall themes.

I was particularly interested in the chapter on California Oak Savanna, as I know more about this vegetation than the other types in the book. The floristic information is less detailed compared to many chapters. Other authors provided species lists, ordinations and/or other summary information, which I liked. This chapter will not serve as a replacement for Jim Griffin's excellent treatment in *Terrestrial Vegetation of California,* at least among more botanically-oriented readers. The Savanna chapter has a range management perspective, and there is considerable detail on this important, practical topic. However, the related, complex subject of oak regeneration is not treated in enough detail. Answers to the cause of apparent failure of blue and valley oaks to regenerate saplings, and even the significance of the apparent failure are multifaceted, and still unclear. But I think more evidence from additional studies that have been undertaken should have been mentioned in the Chapter. For example, the work of K. Danielsen suggesting improved regeneration of Valley Oak with germination in native versus annual grassland, and the extensive regeneration studies performed for the State of California by T. Swieki. It would also have been appropriate to include Garry Oak woodland, even

though it extends well north of California. Finally, I found 3 typo's/mistakes, which makes me wonder how many went unnoticed in other chapters.

I think the most significant contributions of this book are the descriptions of unique, edaphic community types that many vegetation ecologists are unfamiliar with, the integration of plant and animal ecology, and the conservation and management considerations. Compared to typical community descriptions, there is greater discussion of subjects such as endemism, animal interactions, and the widespread management problem of how to determine and achieve an appropriate fire regime. It is interesting and worthwhile to look at these phenomena from the many different aspects and perspectives found in this book.

—DENNIS C. ODION. Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93106.

Terrestrial ecoregions of North America: A conservation assessment. By Taylor Rickets, Eric Dinerstein, David Olsen, Colby Loucks et al. 1999. Island Press. Covelo, California. 485 pp.

When I first saw this book my initial feeling was that this was yet another way to classify ecosystems similar to the U.S. Forest Service ECOMAP (Bailey et al. 1994) or Omernik (1995) approach. However, as I probed the pages I found the book was indeed not only an attempt to divide up the continent into ecologically based units, but most importantly, a true analysis of biological and conservation traits using the 116 ecoregions as study units. By defining the ecoregions and having specialists in various taxonomic groups address basic conservation attributes of each ecoregion, the editors have come up with the first uniform treatment for the continent of these principal building blocks of ecological assessment.

Within the last two years this book and The Nature Conservancy's Precious Heritage (Stein et al. 2000) have arrived and addressed similar issues of national/continental scale conservation. Both are valuable additions to the literature. However, Terrestrial Ecoregions of North America is by far the more scholarly and amenable for use as an actual conservation biology tool for the North American Continent. Precious Heritage, with its glossy format and beautifully illustrated examples of the biota, is pitched to the neophyte who needs to be educated on the urgency of conservation needs and on an overall awareness of the biotic distinctiveness of the United States. Terrestrial Ecosystems is a more utilitarian (and less costly) book. The photos of animals and plants are minimal and not particularly

well reproduced. However the numerous multi-color maps of the continent are clean and effective.

One of the greatest attributes of the Terrestrial Ecosystems book is its adherence to the standardized and uniform division of ecoregions. These ecoregions were defined in a systematic way that is well described in the first chapters. The rational for defining them anew, in lieu of adopting an existing ecoregional classification, is based on the lack of existing uniform treatments for ecoregions covering the full geographic extent of North America. However, adherence to previously defined units where possible is strong, particularly Omernick's (1995). Using the ecoregions, instead of a combination of ecological and political (states, counties) geographic criteria for judging conservation importance, as is the case in Precious Heritage, the book provides a even-handed and readily comperable method of assessing the entire area.

The standardized assessment approach involves a hierarchical division of the continent into realms (3), biogeographical zones (5), 10 major habitat types, and 116 ecoregions. Each of these is given a set of discriminators broken into biological distinctiveness criteria and conservation status criteria. The former include species richness, endemism, rare ecological or evolutionary phenomena, and rare habitat types. The latter include habitat loss, remaining habitat blocks, degree of fragmentation, degree of protection, and future threat. Derived from these criteria are: 1) a biological distinctiveness index, and 2) a conservation status index, which are integrated into five main categories ranging from "globally outstanding ecoregions requiring immediate protection" to "bioregionally and nationally important ecoregions requiring protection of representative habitat blocks and proper management elsewhere for biodiversity conservation." Richness and endemism is analyzed for representative taxa for which sufficient information exists. These include amphibians, birds, butterflies, mammals, vascular plants, reptiles, and land snails. Subdivisions of these major taxonomic groups are also treated including conifers, trees, and tiger beetles. Special features such as subterranean karst biodiversity are also discussed.

The biological assessment elucidates some very interesting facts. Though it is brought out that if politically defined, California leads all other conterminous states in species richness and endemism, the division of the general California area into 12 distinct but relatively small ecoregions has moved the individual ecoregions within or partially within the Golden State into the second tier with respect to several criteria. These include total endemism of all taxa (leaders are the southeastern conifer forests of Florida and adjacent states, and the Colorado Plateau). Bird richness and endemism are lead by southwestern US ecoregions including the Chihua-

huan and Sonoran Deserts. The southeast U.S. is leader in amphibian and snail richness and diversity. Mammal richness is also centered on the Colorado Plateau and the Chihuahuan Desert, while surprisingly mammal endemism is greatest in the Sierra Nevada and the California interior chaparral and woodlands. Many patterns reflect the general trends of tropical diversity. For example, the southwestern border ecoregions lead in butterfly and reptile diversity and endemism.

Perhaps most interesting to you may be the vascular plant patterns, which show the southeastern mixed forests lead the nation in richness with over 3100 species, while the most diverse ecoregion in California is the Mojave Desert with about 2300–2400 species. Vascular plant endemism is lead by the Colorado Plateau and the southeastern conifer forests with over 200 species, while the California ecoregions having highest endemism include the Klamath Province and the California interior chaparral and woodlands, both with between 111 and 150 species. Note this analysis is based on full species (no subspecific taxa) as determined by John Kartesz.

Turning to the conservation status of ecoregions, portions of California do rank among the most threatened including the Great Valley—deemed to have no remaining large blocks of habitat. The Great Valley, the Northern California coastal forests, and the California Coastal sage and chaparral all rank among the most critically imperiled of ecoregions in the conservation snapshot analysis. California also has the unfortunate distinction of containing the greatest number of introduced vascular plant taxa in any ecoregion in its interior chaparral and woodlands ecoregion (879 species).

In the synthesis of biological distinctiveness and conservation status California contains six ecoregions (more than any other state) that are considered globally outstanding requiring immediate protection of remaining habitat and extensive restoration. These are: Klamath-Siskiyou forests, Northern California coastal forests, Sierra Nevada forests, California interior chaparral and woodlands, California montane chaparral and woodlands (includes the Transverse and Peninsular ranges), and the California coastal sage and chaparral.

The main body of the book concludes with a list of the dozen highest-ranking ecoregions in need of immediate attention. The authors compare the relative amount of attention that the Florida Everglades has received with these additional ecoregions, and suggest that all of these are as worthy of attention as the Everglades. Three of these are in California; Coastal sage and chaparral, Klamath-Siskiyou, and Sierra Nevada forests.

Recommendations for the protection of these ecoregions are listed in a 10-point plan. These points, though inherently reasonable and rational,

will have different likelihood of success unless political climates change. For example, completing networks of last remaining habitat in a system of reserves is a easier goal to achieve than allowing fire to play its critical role in maintaining biodiversity or restricting livestock grazing in a number of ecoregions.

Although the core of the book is a conservation assessment (104 pages), the largest portion of the book is devoted to six appendices, the largest of which is a detailed account of each of the 116 ecoregions written by local experts. Other appendices detail the methods of the calculations used to arrive at the biological distinctiveness and conservation ranks, and also include specific lists of richness, endemism for each of the taxonomic groups treated by ecoregions. Appendix F is more than twice as lengthy as the main portion of the book. It contains individual summaries of each ecoregion and is written and/or edited by a group of local experts. (Robin Cox, David Olsen, Bob Holland, and John Sawyer have co-authored a number of the California ecoregions).

My criticisms of the book are relatively minor. As the book is titled a conservation assessment of North America, one would expect to see a detailed treatment that includes not only the US and Canada, but Mexico down to the isthmus of Tehuantapec. In fact although a good map of Mexican ecoregions is displayed, there is insufficient information to afford a detailed analysis of the Mexican ecoregions. Although the treatments of each ecoregion in Appendix F are valuable, they are somewhat uneven in scope and content. I was generally satisfied with those I am most familiar with. However, some inconsistencies remain. For example, some of the best treatments include detailed point-by-point descriptions of what conservation actions need to be taken (including specific locations that need protection), while other areas are not specifically addressed in this way.

As with many good hierarchical treatments, the next step becomes clear. For each of these ecoregions a similar local level assessment needs to be done. The Nature Conservancy is doing this work on an ecoregional level throughout much of California and the rest of the United States. Although the hierarchy in this book stops at the 116 ecoregions, the Bailey ecoregions (1994) do have a more complete nesting of hierarchies down to very local level a geographic scale down to the sub-watershed or so-called ecological land unit. The ecological subsection map and descriptions produced for California (Miles and Goudey 1997) has great conceptual valuable in this regard, yet similar detailed treatments have not been done for all of the country.

I recommend this book for a lucid, scientific approach to conservation at the continental scale. I

intend to take it with me whenever I travel throughout the continent, as it not only affords a clear strategy, but also is a valuable biogeographical summary of information that stands alone in its own right.

—TODD KEELER-WOLF. Senior Vegetation Ecologist, Department of Fish and Game, 1416 9th St. 12th Floor, Sacramento, CA 95814.

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BAILEY, R. G. P. E. AVERS, T. KING, AND W. H. MCNAB. (eds.). 1994. Ecoregions and sub-ecoregions of the United States. Washington D.C., USDA Forest Service.

MILES S. R. AND C. B. GOUDEY. 1997. Ecological subregions of California: section and subsection descriptions. USDA Forest Service Pacific Southwest Region R5-EM-TP-005.

OMERNIK, J. M. 1995. Ecoregions: a framework for managing ecosystems. George Wright Forum 12(1):35–51.

STEIN, B. A., L. S. KUTNER, AND J. S. ADAMS. 2000. Precious Heritage: The Status of Biodiversity in the United States. Oxford University Press. 416 pp.

Botany Grads Meet at Chico State

The 19th California Botanical Society Graduate Student Meetings, for students studying any aspect of plant sciences, was hosted by the Department of Biological Sciences at Chico State University on 17 February 2001. Local Botany graduate student Leah Mahan, with some support by Rob Schlising, planned and organized talk sessions and oversaw this bienniel event where graduate students share their research and ideas in a day of formal talks and discussions with their colleagues. There were 31 abstracts submitted by students from Claremont Graduate University/Rancho Santa Ana Botanical Garden; California State University, Fullerton; University of California, Santa Barbara; California Polytechnic State University, San Luis Obispo; San Francisco State University; University of California at Berkeley; Humboldt State University; University of Kentucky; and Chico State University. One morning session was followed by two concurrent sessions in the afternoon, with talks categorized as research that was 1) completed, 2) in progress, or

3) proposed. Graduate students from Chico State and elsewhere chaired all sessions, or served as judges to evaluate talks in each of the three categories.

Awards of books and memberships in the California Botanical Society were presented at the annual meeting and banquet of the Society, held on campus that evening. First place winners for talks were Christopher Adams, University of Kentucky (completed—"Seed dormancy in *Aristolochia californica*"); Justin Whittal, UC Santa Barbara (in progress—"Key innovation and rapid radiation among the columbines: insights from another chloroplast region and introns of three nuclear genes"); and Gavin Blosser, Chico State (proposed—"Diversity and characterization of arbuscular mycorrhizal fungi in the soils of vernal pools in northern California"). Serpentine plant expert, Dr. Arthur Kruckeberg, of the University of Washington, gave the address after the banquet on "The Influence of Geology in Shaping the California Flora."

Talks Presented at the 19th California Botanical Society Graduate Student Meetings

Adams, Christopher A. School of Biological Sciences, University of Kentucky, Lexington, KY 40506. SEED DORMANCY IN *ARISTOLOCHIA CALIFORNICA* (ARISTOLOCHIACEAE). (Completed)

Bell, Hester L. Department of Botany, Claremont Graduate University and Rancho Santa Ana Botanical Garden, 1500 North College Ave., Claremont, CA 91711. RESPONSE OF *SPOROBOLUS VIRGINICUS* (GRAMINEAE) TO SALINITY. (Completed)

Blosser, Gavin D. Department of Biological Sciences, California State University, Chico, CA 95929. DIVERSITY AND CHARACTERIZATION OF ARBUSCULAR MYCORRHIZAL FUNGI IN THE SOILS OF VERNAL POOLS IN NORTHERN CALIFORNIA. (Proposed)

Bradford, Darhl L. Department of Biological Sciences, California State University, Chico, CA 95929. THE HYBRIDIZATION OF CALIFORNIA SYCAMORE (*PLATANUS RACEMOSA*) AND THE LONDON PLANE TREE (*PLATANUS × ACERIFOLIA*) IN CALIFORNIA'S RIPARIAN WOODLAND. (In Progress)

Bushakra, Jill M. Department of Biological Sciences, California Polytechnic State University, San Luis Obispo, CA 93407. GENETIC DIVERSITY AND PHYLOGENY OF *CIRSIUM OCCIDENTALE*. (In Progress)

Cerros-Tlatilpa, Rosa. Department of Botany, Claremont Graduate University and Rancho Santa Ana Botanic Garden, 1500 North College Ave., Claremont, CA 91711. SYSTEMATICS OF *ARISTIDA* (GRAMINEAE). (In Progress)

Douhovnikoff, Vladimir. Department of Environmental Science, Policy & Management, University of California at Berkeley, 4927 Happy Valley Rd., Lafayette, CA 94549. THE IMPORTANCE OF CLONING IN *SALIX EXIGUA* (In Progress)

Ellberg, Sherry R. Department of Biological Sciences, California State University, Chico, CA 95929. QUANTITATIVE TRAIT LOCI ANALYSIS IN *CLARKIA LINGULATA* AND *CLARKIA BILOBA* SSP. *AUSTRALIS*. (In Progress)

Fry, Danny, L. Department of Biological Sciences, California Polytechnic State University, San Luis Obispo, CA 93407. EFFECTS OF A PRESCRIBED FIRE ON OAK WOODLAND STAND STRUCTURE. (In Progress)

Ganong, Constance K. Department of Biology, San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132. PHYLOGENETIC ANALYSES OF *PHACELIA* SECTION *MILTITZIA* USING MORPHOLOGICAL AND MOLECULAR DATA. (In Progress)

Gehrung, Loren. Department of Biological Sciences, California State University, Chico, CA 95929. INVESTIGATIONS IN THE GENUS *VACCINIUM,* SECTION *MYRTILLUS,* IN NORTHERN CALIFORNIA AND SOUTHERN OREGON, INCLUDING RESOLUTION OF THE TAXONOMIC STATUS OF *VACCINIUM COCCINEUM* PIPER BY RAPD ANALYSIS. (Completed)

Griffith, Patrick M. Department of Botany, Claremont Graduate University and Rancho Santa Ana Botanical Garden, 1500 North College Ave., Claremont, CA 91711. NATURAL INTERSPECIFIC HYBRIDIZATION IN *OPUNTIA* OF THE NORTHERN CHIHUAHUAN DESERT REGION. (Completed)

Hendrick, Mike B. Department of Biological Sciences, California State University, Chico, CA 95929. ENVIRONMENTAL FACTORS AND THEIR EFFECTS ON FLORAL COMMUNITY STRUCTURE IN THREE MONTANE MEADOWS IN BUTTE COUNTY, CALIFORNIA. (Completed)

Honer, Michael. Department of Botany, Claremont Graduate University and Rancho Santa Ana Botanical Garden, 1500 North College Ave., Claremont, CA 91711. A FLORA OF THE GLASS MOUNTAIN REGION, MONO COUNTY, CA. (In Progress)

Kashani, Nasser. Department of Environmental Science, Policy & Management, University of California at Berkeley, 4927 Happy Valley Rd., Lafayette, CA 94549. EXTENT OF GENETIC DIFFERENTIATION BETWEEN *QUERCUS PARVULA* VAR. *SHREVEII* AND *Q. WISLIZENII.* (Completed)

Karr, Stephen J. Department of Biological Sciences, California State University, Chico, CA 95929. INFLUENCE OF CARBON TO NITROGEN RATIO ON THE GENETIC CONTROL OF XYLOGENESIS IN *ARABIDOPSIS THALIANA.* (Proposed)

Kirk, Paul. Department of Biological Sciences, California State University, Chico, CA 95929. AFLP ASSESSMENT OF PUTATIVE *JUGLANS HINDSII* IN RIPARIAN FORESTS OF NORTHERN CALIFORNIA. (Proposed)

LaDoux, Tasha. Department of Botany, Claremont Graduate University and Rancho Santa Ana Botanical Garden, 1500 North College Ave., Claremont, CA 91711. COALESCENCE OF S-ALLELES IN *PHYSALIS CINERASCENS* (DUNAL) A.S. HITCHC. (Proposed)

Mahan, Leah M. Department of Biological Sciences, California State University, Chico, CA 95929. FACTORS AFFECTING THE SURVIVAL OF *HEMIZONIA FITCHII* (ASTERACEAE) IN THE NORTHERN SACRAMENTO VALLEY OF CALIFORNIA. (In Progress)

McDill, Joshua R. Biology Department, San Francisco State University, 1600 Holloway Ave, San A COMPARATIVE ANATOMICAL STUDY OF *LINANTHUS* AND RELATED GENERA (POLEMONIACEAE). (In Progress)

McGlaughlin, Mitchell. Department of Botany, Claremont Graduate University and Rancho Santa Ana Botanical Garden, 1500 North College Ave., Claremont, CA 91711. GENETIC VARIABILITY OF REINTRODUCED POPULATIONS OF PINK SAND VERBENA. (Completed)

McGraw, Jodi M. Department of Integrative Biology, University of California, Berkeley, CA 94720. FIRE SUPPRESSION, TREE ENCROACHMENT, AND THE SPREAD OF EXOTIC SPECIES INFLUENCE THE PERSISTENCE OF TWO ENDANGERED PLANTS IN CALIFORNIA. (In Progress)

Menke, Marck. Department of Biology (Ecology and Systematics), San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132. A MOLECULAR BASED PHYLOGENETIC ANALYSIS OF THE WOODY HYDROPHYLL CLADE. (Proposed)

Parks, David T. Department of Biological Sciences, California State University, Chico, CA 95929. EVOLUTIONARY RELATIONSHIPS OF *ARCTOSTAPHYLOS MEWUKKA* AND ASSOCIATED SPECIES. (In Progress)

Phipps, Frances A. Department of Biological Sciences, California State University, Chico, CA 95929. POPULATION GENETIC ANALYSIS OF *HOWELLIA AQUATILIS* (CAMPANULACEAE). (In Progress)

Rentz, Erin D. Biology Department, San Francisco State University, 1600 Holloway Ave, San Francisco, CA 94132. EFFECTS OF BURNING ON THE ANATOMICAL STRUCTURE OF *CORYLUS CORNUTA* AND *XEROPHYLLUM TENAX,* PLANTS COMMONLY USED IN CALIFORNIA INDIAN BASKETRY. (Proposed)

Stewman, Casey J. Department of Biological Sciences, Humboldt State University, Arcata, CA 95521. ENCROACHMENT PATTERNS OF DOUGLAS-FIR INTO OAK WOODLANDS IN THE CENTRAL WESTERN KLAMATH REGION. (Completed)

Timme, Ruth E. Department of Biology (Ecology and Systematics), San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132. A MOLECULAR PHYLOGENY OF THE GENUS *POLEMONIUM* (POLEMONIACEAE). (In Progress)

Wendel, Heather E. Department of Biological Science, California State University, Fullerton 800 N. State College Ave., Fullerton, CA 92831. COMPETITION BETWEEN INVASIVE EXOTIC ANNUALS AND NATIVE ENDANGERED *ERIASTRUM DENSIFOLIUM* SSP. *SANCTORUM* (POLEMONIACEAE) SHRUBS. (Proposed)

Willyard, Ann M. Department of Biological Sciences, California State University, Chico, CA 95929. MAPPING A DISEASE-RESISTANCE GENE IN SUGAR PINE AND WESTERN WHITE PINE. (In Progress)

Whittall, Justen, B. Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA. KEY INNOVATION AND RAPID RADIATION AMONG THE COLUMBINES: INSIGHTS FROM ANOTHER CHLOROPLAST REGION AND INTRONS OF THREE NUCLEAR GENES. (In Progress)

Northwest Plant Hunters Series: Life of Botanist Louis F. Henderson

The Native Plant Society of Oregon proudly announces the publication of NPSO Occasional Paper Number 2, "Louis F. Henderson (1853–1942): the Grand Old Man of Northwest Botany," by Dr. Rhoda M. Love of Eugene.

The peer-reviewed paper has been formatted as a 64-page booklet with 56 historic and modern images—many never before published. It is carefully researched, with 133 notes. Also included are a chronology of Henderson's life, notes on many of his important collections, a list of his publications, and a list of plants named for Henderson. The research took nearly three years and extended throughout the Pacific Northwest as well as to Mississippi, Cornell University, The Chicago Field Museum, the Smithsonian Institution, and the Jepson Herbarium at Berkeley. The Occasional Paper is a much-expanded version of Dr. Love's earlier essay on Henderson which appeared in Pacific Northwest Quarterly last year.

Henderson lived through the Civil War in Mississippi only to see his lawyer father murdered in New Orleans during the Reconstruction period. Young Louis was educated at Cornell, studying botany under David Starr Jordan, later President of Stanford. He came west in 1874 and moved to Portland in 1877 to take up a teaching post. He began his botanizing in Washington and Oregon at that time. Soon after, Henderson married fellow teacher Kate Robinson and the couple had two daughters. Henderson had several careers in botany in the Northwest including that of Professor of Botany at the University of Idaho from 1893 to 1908. It was during this time that his herbarium burned, destroying an estimated 85,000 specimens. At the age of seventy-one he became Curator of the Herbarium of the University of Oregon and remained for 15 years, greatly increasing the collection. Approximately 30 species were named for Henderson; 16 bear his name today.

The Native Plant Society of Oregon, a non-profit organization, has advanced funds for the printing and mailing of 200 copies of the Henderson Occasional Paper. The Native Plant Society wishes to recoup its investment in a timely fashion, thus mail orders will be accepted starting immediately. The cost is $10.00 per copy which includes mailing and handling. Orders will be filled as soon as received.

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Proceedings volume—*2ⁿᵈ Interface Between Ecology and Land Development In California*. Edited by J.E. Keeley, M.B. Keeley and C.J. Fotheringham. 2000. U.S. Geological Survey.

Request a copy from either: Jon_Keeley@usgs.gov or Sequoia National Park, 47050 Generals Highway, Three Rivers, CA 93271.

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AMONG- AND WITHIN-PROVENANCE VARIABILITY OF *PINUS PONDEROSA* (PINACEAE) SEEDLING RESPONSE TO LONG-TERM ELEVATED CO$_2$ EXPOSURE

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Abstract

Among- and within-provenance variability in growth and physiological performance were investigated in *Pinus ponderosa* Dougl. ex P. Laws. seedlings subjected to ambient or elevated carbon dioxide (ambient + 175 µLL^{-1} or ambient + 350 µLL^{-1} CO$_2$) for 16 months. Among-provenance variability was studied with bulk-collection sources from 5 different physiographic regions of California. Within-provenance variability was investigated with three half-sibling families from a common physiographic locale. Regardless of source, stem volume increased at ambient + 175 µLL^{-1} CO$_2$, but further increase in CO$_2$ to ambient + 350 µLL^{-1} resulted in a variety of stem volume responses with about equal numbers of sources showing either no change or slight increases. Physiological responses to elevated CO$_2$, including decreased efficiencies of photochemical transfer (F$_v$/F$_m$), no change in stomatal conductance, and increased photosynthesis and water-use efficiency, were consistent among half-sibling families. Thus, for this limited survey, there was little evidence for within-provenance variation in physiological response to elevated CO$_2$. Among- and within-provenance variability in growth response to CO$_2$ suggests differing genetic control of carbon acquisition and allocation mechanisms among sources of *P. ponderosa*. Understanding the extent and sources of intraspecific variation in growth and physiological responses to elevated CO$_2$ is a critical need in developing management strategies that account for future altered environments.

Introduction

The potential impacts of increasing atmospheric CO$_2$ concentration, related increasing mean temperatures, and changing precipitation patterns on the sustained functioning and productivity of forest ecosystems are not well known. After many years of research on forest tree responses to elevated CO$_2$ concentrations, the level of uncertainty in estimating these impacts remains high as experimental exposures of tree species to elevated atmospheric CO$_2$ has revealed a diverse range of responses (Gunderson and Wullschleger 1994).

Elevated CO$_2$ generally results in increased carbon assimilation and increased growth of young trees. Growth enhancement results from physiological adaptations that optimize photosynthetic carbon acquisition and allocation processes (Acock and Al-

len 1985; Eamus and Jarvis 1989; Pushnik et al. 1995). In general, growth responses consist of increased biomass allocated among different plant structures (e.g., foliage, stems and roots) and may result in shifts in root:shoot ratios (Callaway et al. 1994; Walker et al. 1995). Growth responses vary widely among genera (Tolley and Strain 1984), among species within the same genus (Rogers et al. 1994), and intraspecifically (Houpis et al. 1995). Differences among taxa suggest that multiple factors, possibly under genetic control, may be operating to determine the physiological and growth responses to elevated atmospheric CO$_2$ concentrations.

There have been few investigations of intraspecific variation in CO$_2$ responses for forest trees. Published studies have addressed intraspecific variation in terms of response differences among ecotypes (e.g., *Pinus ponderosa*, Callaway et al. 1994; DeLucia et al. 1994; Houpis et al. 1995), among provenances (e.g., *Picea mariana*, Johnsen and Ma-

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jor 1998) and within stands (e.g., *Betula alleghaniensis,* Wayne and Bazzaz 1995). Typically, studies to date have addressed relatively narrow sources of variation by either considering relatively few genotypes or relatively distinct ecotypes. The works of Johnsen and others with *P. mariana* are among the most robust studies of provenance × CO_2 interactions based on the number and range of genetic families considered (Johnsen and Seiler 1996; Johnsen and Major 1998).

Pinus ponderosa Dougl. ex Laws. is common throughout much of the forested western United States, and as such is of great ecological and economic importance. Pacific and Rocky Mountain varieties of *P. ponderosa* differ in growth and physiological responses to elevated concentrations of CO_2 (Surano et al. 1986; Houpis et al. 1988; Surano and Kercher 1993). Sierra Nevada seedlings demonstrated substantially greater increases in stem height and stem volume at CO_2 concentrations of 150 and 300 μLL^{-1} above ambient than did Rocky Mountain seedlings. Following two years of growth under elevated CO_2, seedlings of Rocky Mountain origin had shed most of their two-year-old needles and a large percentage of their 1-year-old needles. In contrast, seedlings of Sierra Nevada origin maintained more age classes of foliage at elevated CO_2 concentrations but displayed extensive mid-needle abscission in older age classes and a twisting deformation of current-year needles.

In California, *P. ponderosa* is found in several diverse physiographic/climatic regions including the north-south oriented coastal and Sierra Nevada mountain ranges, the Klamath Mountains of the northwest, the Modoc Plateau in the northeast, and in the transverse mountain ranges of southern California. Climates vary from temperate and humid along the northern Pacific coast, to cold and semiarid in the eastern Sierra Nevada (Bailey 1994). *Pinus ponderosa* occurs as a component of four major California forest types in which species composition varies with physiographic and climatic site characteristics: Pacific ponderosa pine, interior ponderosa pine, Sierra Nevada mixed conifer, and Pacific ponderosa pine–Douglas-fir (Eyre 1980). Seed zone and breeding zone stratification in the U.S.F.S., Pacific Southwest Region breeding program (Kitzmiller 1976) implies that physiographically or climatically adapted sub-populations of *P. ponderosa* may have evolved. It is unknown if subpopulations differentially adapted to climate and physiography will respond to future atmospheric carbon dioxide concentrations similarly or differently.

Our study surveyed variability in *P. ponderosa* seedling responses to elevated CO_2, both among provenances (geographic locations of natural origin) representative of the species occurrence in several major forest types of California, and within a provenance using genotypes of *P. ponderosa* having high growth potential. Physiological and growth parameters were used to assess response variability at multiple scales of plant structure and function. Elucidation of underlying sources of intraspecific variability at both physiological and whole-plant scales is a critical step in the development of process and ecological models for the assessment of climate change impacts on forest community dynamics. Predictions of genotype and population response to climate change can be used to develop genetic resource and silvicultural management strategies to ensure the maintenance of genetic diversity, ecosystem integrity, and forest productivity in a future environment.

Materials and Methods

Plant material and growth conditions. Pinus ponderosa seedlings from seed sources of different geographic origin were exposed to various atmospheric CO_2 concentrations at the Lawrence Livermore National Laboratory (LLNL) exposure facility. Among-provenance variability was evaluated with seedling sources originating as bulked seed collections from stands in each of 5 different physiographic regions in California. Each bulk collection was made up of seed from 25 to 50 individuals per stand, with stands typically being less than 25 ha in size. These 5 sources included two coast range provenances (Mendocino, north coastal range, and Santa Clara, central coastal range), a provenance from the southern California transverse mountain ranges (San Bernardino), and two provenances from the Sierra Nevada (El Dorado, westside Sierra, and Tahoe, east-side Sierra). Although ponderosa pine is a common species in forests of each, the 5 physiographic regions have distinct climatic, geologic and vegetative characteristics that are reflected in different ecological classifications (Table 1; Fig. 1). Within-provenance variability was assessed using seedlings of 3 half-sib families (families 3087, 3088, and 3399), obtained from maternal parents located within a 2-km radius at ca. 1500-m elevation in the central Sierra Nevada of California (El Dorado National Forest). Growth and physiology of the 3 half-sib families have been intensively characterized in previous studies examining genotypic variation in ponderosa pine response to ozone and acid deposition (Benes et al. 1995; Anderson et al. 1997; Momen et al. 1997).

Bulk-collection seedlings were obtained as 1-0 bare-root stock from the California Department of Forestry nursery in Davis, California. Half-sib seedlings were obtained as one-year-old container stock from the U.S.F.S. Genetic Resource Center in Chico, California. Upon receipt at LLNL, the seedlings were transplanted to 12.8-L pots containing a loam soil mix formulated to optimize pine seedling growth (American Soil Co., Berkeley, CA). The soil mix, which had good aeration and high nutrient and water-holding capacity, consisted of 2 parts clay (pulverized expanded shale), 3 parts red lava

TABLE 1. ECOLOGICAL CLASSIFICATION AND CLIMATIC CHARACTERISTICS OF SEEDLING PROVENANCES AND THE COMMON-GARDEN TEST SITE. Seed zone designations are those of the USDA Forest Service, Region 5 Tree Improvement Program. Ecological classification is according to the USDA Forest Service ECOMAP program (McNab and Avers 1994). Climatic descriptions apply to the ecological classification subsections from which the provenance collections were made and are based on subsection descriptions by Goudey and Smith (1994) and Miles and Goudey (1997).

| | Location | | | | Mean annual climatic conditions of subsection | | |
| | USFS seed zone | Eleva-tion (m) | Ecological classification | | Precipita-tion (cm) | Temper-ature (°C) | Frost-free period (d) |
Source			Section	Subsection			
			Bulk-collections (among provenance)				
Mendocino	351	610	Northern California Coastal Range	M261Ba	100–305	5.4–12.3	100–200
Santa Clara	097	150	Central California Coastal Range	M261Af	50–150	10.0–14.4	250–300
San Bernardino	994	1525	Southern California Mountains and Valleys	M262Bh	75–100	4.4–10.0	150–200
Tahoe	772	1525	Sierra Nevada (east-side)	M261Ej	50–100	1.7–7.2	25–75
El Dorado	526	915	Sierra Nevada (west-side)	M261Eg	100–205	7.2–12.8	100–150
			Half-siblings (within provenance)				
Families 3087, 3088, 3399	526	1370	Sierra Nevada (west-side)	M261Eg	100–205	7.2–12.8	100–150
			LLNL Common Garden Test Site				
		30	Great Valley	262Aq	20–41	15.0–16.7	250–275
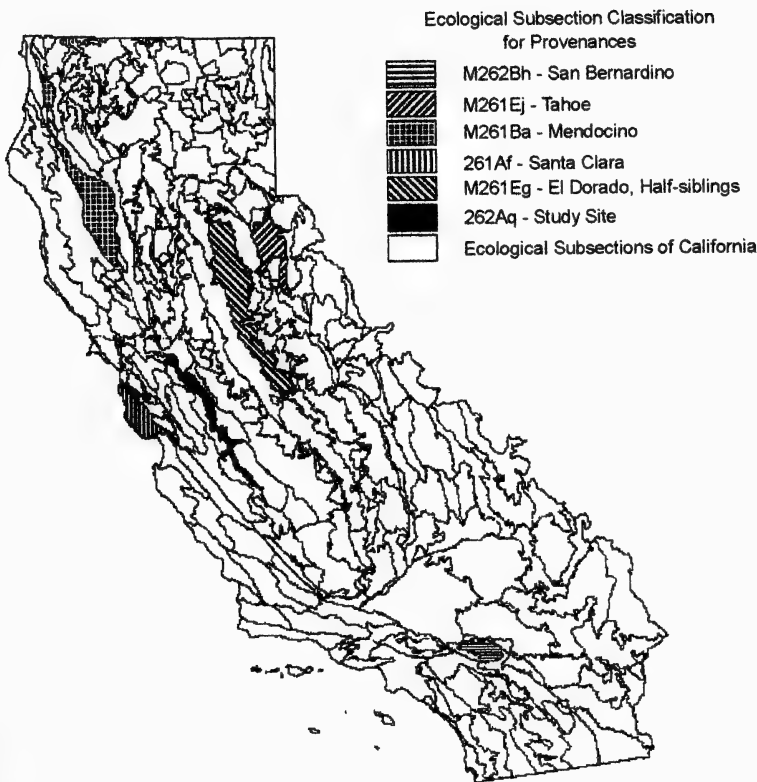
FIG. 1. Ecological subsections of California. Shaded areas represent subsections from which bulk-collection or half-sibling seedlings originate, and the subsection in which the study site exists.

rock (ground to particle sizes less than 2 mm diameter, resulting in a coarse sand texture), 1 part colma sand, and 3 parts bark. The seedlings were grown for 2 years prior to CO_2 fumigation. At the start of the experiment, seedling were distributed to 18 standard outdoor open-top exposure chambers (3-m diameter and 3-m height; Rogers et al. 1983). All seedlings were watered at 2-3 day intervals and were fertilized at 4–6 week intervals during the growing season using a one-half strength Hoagland's solution.

CO_2 treatments. Seedlings were exposed to 3 CO_2 concentrations including ambient (ca. 350 μLL^{-1} CO_2), ambient + 175 μLL^{-1} CO_2, and ambient + 350 μLL^{-1} CO_2 to cover the range from existing mean concentration through the doubling in mean concentration expected to occur within the 21st century. The open-top chamber CO_2 concentrations were monitored using dedicated CO_2 analyzers (Horiba Model PIR-2000). Analyzers were zero- and span-checked daily and under went a multi-point calibration monthly. Chamber atmospheres were sampled 12 times per hour at canopy height, at the center of the chamber. The chamber CO_2 concentrations were maintained within ±5% of the treatment concentration, 24 hr per day from April through completion of second season stem elongation in July for a total of 16 months.

Seedling growth. Seedling total height and basal diameter were measured during September and July, following cessation of growth, in the first and second seasons. Pre-experimental height was determined from leaf scars at the base of the stem segment. Estimates of total height and diameter were used to calculate an index of stem volume (π * radius^2 * height). Total height growth was estimated as the difference between the final and pre-experimental total heights. Stem volume growth was estimated as the difference between first and second season's main stem volumes.

Light harvesting system. The relative photochemical efficiency of electron transport reactions for photosystem II (PSII) was estimated by chlorophyll fluorescence (Long and Drake 1992). Dark-adapted fluorescence measurements were made in situ for both current-year and one-year-old foliage using a portable chlorophyll fluorescence measurement system (CF-1000, Morgan Scientific, Andover, MA). Fluorescence was induced with an excitation light intensity of 750-μmol m^{-2} s^{-1} and fluorescence kinetics was monitored for the subsequent 20 seconds. An index of PSII quantum efficiency was calculated as the ratio of the variable fluorescence component to maximal fluorescence (Fv/Fm; Genty et al. 1989). Measurements were made in July of the second growing season of experimental exposures, in conjunction with gas-exchange sampling.

The concentrations of chlorophyll a and b, and carotenoids were determined for current-year and one-year-old foliage. Following determination of foliar surface area, pigments from foliage samples were extracted in 5 ml of N,N-dimethylformamide in the dark and at 4°C for a period of 14 days (Moran and Porath 1980). Concentrations of the three pigments in the solution were calculated according to Wellburn and Lichtenthaler (1983).

Gas exchange. CO_2 and H_2O vapor flux of one-year-old foliage were measured in July following cessation of current-year needle elongation with a closed-loop photosynthesis system consisting of a portable infrared gas analyzer and microprocessor controller (LI-6200, Licor Inc., Lincoln, NE) coupled to a 0.25 L cuvette. All measurements were made mid-morning (0900–1030) inside the open-top chambers at the growth CO_2 concentration ± 15 μLL^{-1}. Light intensity within the cuvette was maintained at 1000 μmol m^{-2} s^{-1} (above the saturating light intensity for *P. ponderosa*) using a LED array with peak spectral radiation of 670 nm wavelength (QB-2001, Quantum Devices Inc., Barneveld, WI). Mean (± 1 SE) leaf temperature over all gas exchange measurements was 30.1 ± 0.4°C. The mean leaf-air vapor pressure deficit VPD over all gas exchange measurements was 1.48 ± 0.14 kPa. Estimated gas-exchange parameters included net photosynthesis (P_n), stomatal conductance to water vapor (g_{sw}), leaf internal CO_2 concentration (C_i), and photosynthetic water-use efficiency (WUE, net photosynthesis rate/transpiration rate).

Experimental design. The study was conducted using a split-plot design. Three levels of atmospheric CO_2 concentration, the main plot factor, were randomly assigned to 18 open-top chambers to provide 6 replications of each CO_2 concentration. Within each chamber, seedlings of the 3 half-sibling families and 5 bulk-collection sources represented a sub-plot factor. Three seedlings per bulk-collection source and one seedling per half-sib family were grown in each chamber. Growth, fluorescence, and pigmentation responses were measured for all 8 families. Gas-exchange responses to elevated CO_2 were assessed in the half-sibling families only. Separate statistical analyses were performed for among- and within-provenance evaluations.

Significance of genetic source, CO_2 treatment effects, and their interaction on fluorescence and gas exchange parameters were evaluated using ANOVA. Differences with a type I error probability of 0.05 or less were considered significant. Seedling growth responses may be dependent on seedling size at the initiation of CO_2 exposures. Therefore, ANACOV was used to analyze treatment effects on total height growth and stem volume growth with pre-experiment seedling height as a covariate to account for initial variation in seedling size. For those parameters having significant among-provenance or within-provenance effects, linear contrasts were used to determine significant differences between: 1) west-side and east-side Sierra Nevada sources; 2) coast range and Sierra Nevada sources; 3) Sierra

TABLE 2. SEEDLING HEIGHT GROWTH AND VOLUME GROWTH BY SOURCE AND CO_2 FOR HALF-SIB AND BULK-COLLECTION SEEDLING SOURCES. Values are means ± SE for n = 6 observations per source × CO_2 treatment combination. Stem volume values are least-squares means ± SE incorporating an adjustment for variation in pre-treatment total height. Family or provenance means over all CO_2 levels designated by a common letter do not differ statistically (P < 0.05). Probabilities indicate the significance of linear (l) or quadratic (q) CO_2 effects for each source as determined by orthogonal contrasts.

CO_2 Treatment	Bulk-collection seed source						Half-sib seed source			
	N. coastal Mendocino	E. Sierra Tahoe	San Bernardino	C. coastal Santa Clara	W. Sierra El Dorado	All bulk-collections	3087	3088	3399	All half-sibling families
Height growth (cm)										
Ambient	51.9 ± 4.8	39.7 ± 1.6	45.6 ± 5.3	53.3 ± 5.2	43.1 ± 5.2	42.7 ± 5.2	45.1 ± 3.0	66.2 ± 5.3	42.7 ± 5.2	51.3 ± 3.6
Amb + 175	58.6 ± 2.5	41.6 ± 2.6	46.7 ± 8.7	51.7 ± 3.4	50.0 ± 3.3	49.7 ± 2.2	55.1 ± 2.9	75.6 ± 6.6	56.2 ± 4.6	62.3 ± 3.5
Amb + 350	50.5 ± 3.0	38.6 ± 4.5	44.3 ± 4.9	57.4 ± 4.1	50.8 ± 4.6	48.3 ± 2.1	55.6 ± 5.5	65.2 ± 3.4	58.6 ± 3.4	59.8 ± 2.5
All CO_2	53.6[y] ± 2.1	40.0[z] ± 1.7	45.7[yz] ± 3.3	54.1[y] ± 2.0	47.9[yz] ± 2.7		51.9[b] ± 2.5	69.0[a] ± 3.1	52.5[b] ± 3.0	
Prob > H_0	0.138, q	0.625, l	0.750, q	0.460, q	0.183, l	0.652, l	0.137, l	0.100, q	0.028, l	0.032, q
Stem volume growth (cm^{-3})										
Ambient	511 ± 66	341 ± 30	416 ± 38	538 ± 49	429 ± 67	447 ± 25	298 ± 22	530 ± 96	385 ± 132	404 ± 56
Amb + 175	620 ± 45	451 ± 34	594 ± 118	586 ± 49	528 ± 95	556 ± 33	563 ± 69	637 ± 111	479 ± 51	559 ± 46
Amb + 350	622 ± 39	483 ± 44	524 ± 92	871 ± 98	600 ± 67	620 ± 39	634 ± 115	598 ± 82	594 ± 87	609 ± 52
All CO_2	584[xy] ± 30	424[z] ± 25	512[yz] ± 51	665[x] ± 52	519[yz] ± 45		498[a] ± 55	588[a] ± 54	486[a] ± 56	
Prob > H_0	0.151, l	0.068, l	0.171, q	0.001, l	0.102, l	0.004, l	0.017, l	0.758, l	0.112, l	0.022, l

TABLE 3. FOLIAGE PIGMENT CONCENTRATIONS AND PHOTOSYSTEM II EFFICIENCY BY SOURCE AND CO_2 TREATMENT FOR 5 BULK-COLLECTION (AMONG-PROVENANCE) AND 3 HALF-SIB (WITHIN-PROVENANCE) SEEDLING SOURCES. Values are means one standard error of the mean. Source × CO_2 treatment means are based on n = 10–12 observations. Source means averaged over all CO_2 treatments denoted by a common letter do not differ at the P = 0.05 level of significance. Probabilities indicate the significance of linear (l) or quadratic (q) CO_2 effects for each source as determined by orthogonal contrasts.

| | Foliage pigment concentrations and photosystem II efficiency | | | | |
| | Bulk-collection seed source | | | | |
CO_2 Treatment	N. coastal BC5	E. Sierra BC6	San Bernardino BC7	C. coastal BC8	W. Sierra BC9
	Total chlorophyll ($\mu g\ cm^{-2}$)				
Ambient	19.5 ± 1.01	17.8 ± 1.8	20.1 ± 1.7	15.6 ± 1.2	14.8 ± 1.7
Amb + 175	23.7 ± 5.6	17.4 ± 1.2	13.5 ± 1.8	13.6 ± 1.2	12.3 ± 1.1
Amb + 350	16.5 ± 1.3	13.5 ± 1.6	17.7 ± 1.5	15.3 ± 1.4	13.5 ± 1.0
All CO_2	19.9[a] ± 2.0	16.6[ab] ± 0.9	16.9[ab] ± 1.0	14.8[b] ± 0.7	13.5[b] ± 0.8
Prob. > H_0	0.021, q	0.228, l	0.033, q	0.893, l	0.625, l
	Carotenoids ($\mu g\ cm^{-2}$)				
Ambient	9.4 ± 0.4	8.7 ± 0.8	9.1 ± 0.8	7.5 ± 0.5	7.4 ± 0.7
Amb + 175	8.4 ± 0.8	8.0 ± 0.6	6.6 ± 0.7	6.6 ± 0.4	6.1 ± 0.4
Amb + 350	8.3 ± 0.5	7.3 ± 0.6	8.1 ± 0.6	7.1 ± 0.6	6.7 ± 0.4
All CO_2	8.7[a] ± 0.3	8.0[ab] ± 0.4	7.9[ab] ± 0.4	7.1[b] ± 0.3	6.7[b] ± 0.3
Prob. > H_0	0.186, l	0.086, l	0.004, q	0.555, l	0.452, l
	Photosystem II efficiency (F_v/F_m)				
Ambient	0.780 ± 0.070	0.780 ± 0.008	0.767 ± 0.005	0.722 ± 0.022	0.749 ± 0.007
Amb + 175	0.748 ± 0.010	0.759 ± 0.008	0.722 ± 0.009	0.682 ± 0.026	0.688 ± 0.002
Amb + 350	0.776 ± 0.011	0.740 ± 0.009	0.765 ± 0.009	0.707 ± 0.015	0.714 ± 0.017
All CO_2	0.768[a] ± 0.005	0.760[a] ± 0.005	0.752[a] ± 0.005	0.718[b] ± 0.012	0.704[b] ± 0.010
Prob. > H_0	0.079, q	0.040, l	0.010, q	0.060, q	0.015, q

Nevada sources and the San Bernardino source; and 4) coast range sources and the San Bernardino source. Response to CO_2 concentration as a main effect, or within-provenance or family was tested using orthogonal contrasts. Orthogonal contrasts discern responses having either significant linear or quadratic trends over the range of CO_2 treatments. All analyses were performed using PROC GLM of SAS v. 6.11 (SAS 1989).

RESULTS

Foliage-age class variation. Photosystem II efficiencies did not differ among foliage age-classes. In half-sib seedlings, foliage pigment concentrations were significantly greater (P < 0.001) in one-year-old foliage than in current-year foliage. In bulk-collection seedlings, pigment concentrations were slightly greater (P = 0.05–0.09) in one-year-old foliage. Interaction effects of foliage age-class by CO_2 and by genotype were non-significant. From this point forward, results and discussion of PSII and pigmentation results refer to means averaged over both foliage age-classes.

Among-provenance variation. Substantial among-provenance variation in growth was detected. When averaged over all CO_2 treatments, height growth varied from 40 cm for the Tahoe provenance to 54 cm for the Mendocino provenance, and volume

growth ranged from 424 cm^3 for the Tahoe provenance to 665 cm^3 for the Santa Clara provenance (Table 2). Stem volume growth, averaged over all provenances, was 39% greater under ambient + 350 CO_2 than under ambient CO_2. However, stem volume growth responses to elevated CO_2 were only significant for the El Dorado (P = 0.001) provenance (Table 2). In contrast to all other provenances, the stem volume growth of the San Bernardino provenance was greatest in the ambient + 175 CO_2 treatment and tended to decline with further CO_2 increase to ambient + 350 (Table 2). Height growth response to CO_2 was generally non-significant (P = 0.652 over all provenances) and patterns of response to increasing concentration were inconsistent among provenances (Table 2). Pre-treatment height did not contribute significantly to the explanation of variance in height growth and was not included as a covariate in the analysis presented here.

Foliage pigmentation and PSII efficiency also differed significantly among provenances. Total chlorophyll and carotenoid concentrations ranged from 13.5 and 6.7 $\mu g\ cm^{-2}$, respectively, for the El Dorado provenance to 19.9 and 8.7 $\mu g\ cm^{-2}$ for the Mendocino provenance. Photosystem II efficiency (F_v/F_m ratio) ranged from 0.704 for the El Dorado provenance to 0.768 for the Mendocino provenance (Table 3). As with height growth, pigmentation and

TABLE 3. EXTENDED.

		Foliage pigment concentrations and photosystem II efficiency		
Bulk-collection seed source		Half-sib seed source		
All BC	3087	3088	3399	All HS
		Total chlorophyll (μg cm^{-2})		
17.5 ± 0.7	15.8 ± 1.3	15.5 ± 1.5	17.5 ± 1.6	16.3 ± 0.8
16.1 ± 1.3	13.3 ± 1.3	15.9 ± 1.1	16.8 ± 1.0	15.3 ± 0.7
15.5 ± 0.6	11.5 ± 1.1	14.8 ± 1.4	14.7 ± 1.2	13.7 ± 0.7
	13.6[x] ± 0.7	15.4[xy] ± 0.7	16.3[y] ± 0.7	
0.146, 1	0.002, 1	0.361, 1	0.055, 1	0.022, 1
		Carotenoids (μg cm^{-2})		
8.4 ± 0.3	7.6 ± 0.5	7.6 ± 0.6	8.3 ± 0.7	7.8 ± 0.3
7.1 ± 0.3	6.8 ± 0.5	7.6 ± 0.5	8.0 ± 0.4	7.5 ± 0.3
7.5 ± 0.3	5.7 ± 0.5	7.0 ± 0.5	7.2 ± 0.4	6.7 ± 0.3
	6.7[x] ± 0.3	7.4[xy] ± 0.3	7.8[y] ± 0.3	
0.128, 1	0.002, 1	0.239, 1	0.061, 1	0.030, 1
		Photosystem II efficiency (F_v/F_m)		
0.760 ± 0.006	0.750 ± 0.006	0.775 ± 0.009	0.778 ± 0.008	0.768 ± 0.005
0.720 ± 0.009	0.735 ± 0.011	0.740 ± 0.013	0.756 ± 0.012	0.744 ± 0.007
0.740 ± 0.006	0.726 ± 0.014	0.736 ± 0.012	0.744 ± 0.015	0.735 ± 0.008
	0.759[a] ± 0.006	0.750[ab] ± 0.007	0.737[b] ± 0.007	
0.039, 1	0.115, 1	0.012, 1	0.029, 1	0.025, 1

PSII efficiency response to CO$_2$ was inconsistent. Total chlorophyll content of the Mendocino provenance decreased with increasing CO$_2$ from ambient + 175 to ambient + 350. In contrast, total chlorophyll and carotenoid concentrations of the San Bernardino provenance were lowest under the ambient + 175 treatment (Table 3). Pigment concentrations of the other bulk-collection provenances were not significantly impacted by CO$_2$ concentration. In general, PSII efficiency of the bulk-collection provenances were greatest under ambient CO$_2$, and minimal under the ambient + 175 treatment;

the only exception being the El Dorado provenance for which F_v/F_m decreased linearly with increasing CO$_2$ (Table 3).

Contrast analysis indicated that height growth and physiological performance differed significantly between Tahoe and El Dorado provenances; the former having greater pigmentation and PSII efficiency but lesser height growth than the latter (Tables 2, 3, and 4). Growth and physiology of the Sierra provenances could not be distinguished from that of the San Bernardino provenance. In contrast, the coastal provenances had growth rates that were

TABLE 4. CONTRAST ANALYSES OF AMONG-PROVENANCE SEEDLING GROWTH AND PHYSIOLOGY.

	Among-provenance contrast			
Parameter	East-side Sierra vs. West-side Sierra (Tahoe vs. El Dorado)	Coastal vs. Sierra (Mendocino, Santa Clara vs. Tahoe, El Dorado)	Sierra vs. San Bernardino (Tahoe, El Dorado vs. San Bernardino)	Coastal vs. San Bernardino (Mendocino, Santa Clara vs. Santa Barbara)
	Probability > H$_0$			
Height growth	0.018	0.001	0.550	0.005
Volume growth	0.837	0.001	0.701	0.008
Total chlorophyll	0.063	0.403	0.163	0.831
Carotenoids	0.008	0.104	0.149	0.882
Photosystem II efficiency	<0.001	0.786	0.224	0.150

clearly superior to those of the Sierra provenances and the San Bernardino provenance (Tables 2 and 4).

Within-provenance variation. Averaged over all CO_2 treatments, height growth of family 3088 was approximately 32% greater than that of families 3087 and 3399 (Table 2). Volume growth by family 3088 was approximately 18 and 21% greater than that of family 3087 and 3399, respectively (Table 2).

With increasing CO_2 concentration, both families 3087 and 3399 demonstrated a tendency for increased volume growth (linear effect, P = 0.02 and 0.11, respectively, Table 2). In contrast, volume growth by family 3088 was not substantially influenced by CO_2 treatment (Table 2).

Pigment concentrations were greatest for family 3087 and least for family 3399 with the differences among families being significant (P < 0.05). In contrast, PSII efficiency was greatest for family 3399 and least for family 3087 (P < 0.05). In general, pigment concentrations declined with increasing CO_2 concentration from ambient to ambient + 350, but the effect was pronounced in families 3087 and 3399 (13–27% decline) but not in family 3088 (4–8% decline) (Table 3). PSII efficiency ranged from 0.737 for family 3399 to 0.759 for family 3087. However, all families demonstrated a decrease in PSII efficiency with increasing CO_2 concentration from ambient to ambient + 350 that averaged 4% (P = 0.12, 0.01, and 0.03 for families 3087, 3088, and 3399, respectively).

Averaged over all CO_2 concentrations, net photosynthetic rates ranged from 3.9 μmol m^{-2} s^{-1} for family 3088 to 4.5 μmol m^{-2} s^{-1} for family 3399, but differences among families were not significant (Figure 2). Similarly, non-significant family differences in water-use efficiency were also observed. Both net photosynthesis and water-use efficiencies increased significantly with increasing CO_2 in all three families from 71 to 121% (P = 0.01 to 0.05). Thus, gas exchange responses to CO_2 concentration varied less among half-sib families than did pigmentation, PSII efficiency, or growth responses.

DISCUSSION

The substantial among-source variation in elevated CO_2 growth enhancement we observed is consistent with earlier long-term studies comparing Sierra Nevada and Rocky Mountain varieties of *P. ponderosa* (Surano et al. 1986; Houpis et al. 1988). In contrast, greenhouse studies of either 3 black spruce provenances from the species range in Canada or 20 families of black spruce from the New Brunswick province concluded that there were no significant $CO_2 \times$ family effects on growth (Johnsen and Seiler 1996; Johnsen and Major 1998) and that such interactions are more likely to occur under field conditions where other environmental stresses co-occur (Johnsen and Major 1998).
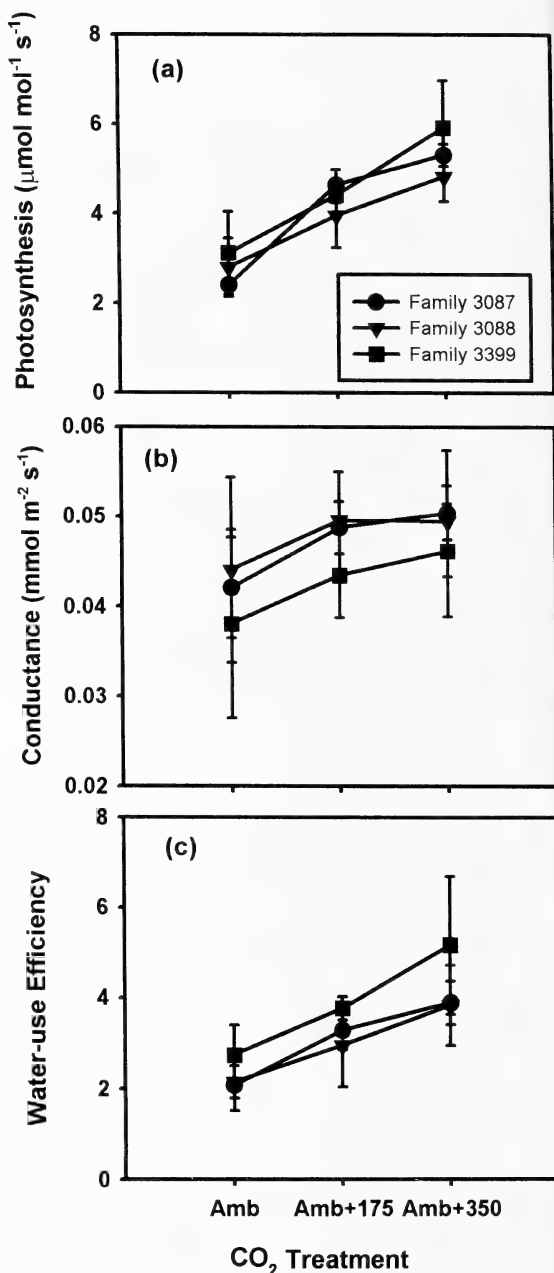

FIG. 2. Foliage gas exchange characteristics by family and CO_2 treatment for three half-sib (within-provenance) seedling sources: a) net photosynthesis, b) stomatal conductance, and c) water-use efficiency. Values are means ± 1 SE of the mean. Source × CO_2 treatment means are based on n = 3 observations. Net photosynthesis response to CO_2 (linear effect) was significant for families 3087 and 3399 (P = 0.010 and 0.012, respectively). WUE efficiency response to CO_2 was significant for families 2087, 3088, and 3399 (P = 0.023, 0.032, and 0.005, respectively). The effect of CO_2 on stomatal conductance was not significant for any family.

The climate of the study site, located in the Great Valley ecological subregion, is characterized by hot, dry summers and mild winters (Table 1). The mean annual temperature is between 14 and 17°C. The higher temperatures and the longer growing season at the common garden site provide reasonable conditions for testing the influence of elevated CO_2 given the coupling between expected global increases in temperature and atmospheric CO_2 concentration. Being a potted seedling study, finite soil water and nutrient resources necessitated irrigation and fertilization to maintain seedling survival and growth. Because of the difficulties in mimicking natural variation in soil resource availability in pots, we chose to supply ample water and nutrients to decrease the potential confounding of limitations of these resources among individual seedlings or among provenances. How potted seedlings would perform relative to seedlings in the ground is difficult to predict without knowledge of soil moisture depletion. At the leaf-level, the high evaporative demand coupled with stomatal aperture being sensitive to leaf-water deficits (Anderson 1991; Anderson and Helms 1994) would probably lead to reduced gas-exchange for seedlings growing either in pots or in the ground. Based on previous studies with planted seedlings of families 3087, 3088, and 3399, the effect of the relatively high leaf temperatures in this study would be to decrease net photosynthetic rates by ca. 5–15% from maximum rates at leaf temperatures of 25 to 26°C (Helms et al. 1994).

The five bulk-collection sources in this study originate in distinct physiographic regions of California and therefore have different degrees of adaptation to the common garden environment. The two sources demonstrating significant or nearly significant response to elevated CO_2, the Tahoe and the Santa Clara sources, respectively, originate in distinctly different environments. Callaway et al. (1994) observed differences in CO_2-induced changes in biomass allocation to foliage and roots of *P. ponderosa* seedlings of 4 geographic origins. As with the variation in volume growth response we observed in bulk-collection sources, the among-population differences they observed were not consistently related to the contrasting montane or desert origins. This implies that response to CO_2 may not be strongly driven by environment of origin, but rather by the genetic potential of the particular populations sampled. The limited number of bulk-collection sources in this study serves to illustrate potential among-population variation across the species range in California, but is not sufficient to characterize variation among populations within geographic regions, and is therefore inadequate for making comparisons of mean population performance between geographic regions. Further, variability in relative growth response to elevated CO_2 among the bulk-collection sources may reflect not only intraspecific variation in CO_2 response mechanisms, but also intraspecific variation in adaptation to the common garden climate. In spite of this potentially confounding effect, the large variation in growth response among bulk-collection sources grown at the common garden site provides a measure of the variability in CO_2 response that exists among provenances of California ponderosa pine. The varied growth responses to elevated CO_2 by three half-sib families indicate that substantial genetic variation exists independent of potential confounding influences of geographic origin. Future efforts to characterize genotype or provenance $\times CO_2$ interaction would benefit by increased numbers of genetic families per geographic region and repetition of the common garden planting at multiple locations over all geographic regions of interest (Weber et al. 1996).

The scale of provenance testing may determine the extent to which genotype $\times CO_2$ interactions are observed. After failing to detect significant provenance $\times CO_2$ interaction among three families of black spruce representing very diverse geographic origins, Johnsen and Seiler (1996) hypothesized that $CO_2 \times$ genotype interactions would become more significant as the genetic background of the families became more similar. Our study supports this hypothesis, as provenance $\times CO_2$ interactions were not evident in comparisons among ponderosa pine bulk-collection sources originating in distinctly different environments, while significant genotype $\times CO_2$ interaction effects were detected for within-provenance comparisons of growth.

At the local scale, all three half-sibling families had similar physiological responses to increasing CO_2 concentration: a decrease in foliage pigmentation; a decrease in photosystem II efficiency; an increase in net photosynthetic rate; and increased water-use efficiency. Thus, processes associated with carbon assimilation were responding to CO_2 concentration similarly, but differences in the efficiencies of assimilate conversion to biomass or differences in the allometric patterns of biomass allocation resulted in significant among-family differences in above-ground growth response.

In summary, carbon assimilation was enhanced with elevated CO_2 for all sources of *P. ponderosa* studied. Enhanced assimilation was accompanied by enhanced volume growth and in some cases enhanced stem elongation. The effect of elevated CO_2 on stem height growth varied both among- and within-provenances. Those sources having more vigorous height growth under ambient CO_2 conditions tended to demonstrate greater enhancement of height growth under elevated CO_2. Assimilation rates were enhanced under elevated CO_2 in spite of decreased light harvesting capacity, suggesting an increase in overall photosynthetic efficiency. Geographic patterns of provenance growth response to elevated CO_2 were not apparent.

Understanding genotypic variability in response to elevated CO_2 is essential to the development of

forest management strategies. Although this study is limited to demonstrating a potential range of variation present in a limited sample, it serves as a model that, if applied with greater sampling intensity, can be used to characterize the adaptive genetic population structure of ponderosa pine in California. Such knowledge can be used by ecologists to better predict the performance of forest tree populations and will guide forest geneticists and resource managers in the breeding and deployment of genotypes that foster genetic diversity and ecosystem resilience in the face of a changing global climate.

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NOTEWORTHY COLLECTIONS

ARIZONA

ENCHYLAENA TOMENTOSA R. Br. (CHENOPODIACEAE).—Maricopa Co., Phoenix, Arizona National Guard Papago Park Military Reservation, northern boundary with Oak Street, disturbed roadside between desert habitat and residential area, found in association with *Salsola tragus, Isocoma acradenia,* and *Chamaesyce polycarpa,* 33°27'30"N, 111°57'30"W, 354 m elev., 26 November 1999, *G. Walters 266* (ASU, NSW). Determined by B. Wiecek (NSW).

Previous knowledge. E. tomentosa was known from a single 1938 specimen from the Tucson Arizona Soil Conservation Service Nursery, *L. Gooding and L. Brinkerhoff 2809* (ARIZ) and this is the first time it has been collected outside of cultivation in Arizona; the second time ever collected in the state. It has been seen growing along the Central Arizona Project canal system and is currently sold at specialty nurseries in the Phoenix Metropolitan area.

Significance. This plant is endemic to Australia where it is drought tolerant but does well in a variety of habitats. The fruits are animal dispersed and germinate prolifically. This combination of characters in a non-native shrub in the Sonoran Desert could potentially render this plant invasive.

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A MORPHOMETRIC ANALYSIS OF THE *LEPTOSIPHON ANDROSACEUS* COMPLEX (POLEMONIACEAE) IN THE CENTRAL AND SOUTH COAST RANGES

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ABSTRACT

The taxonomy of the *Leptosiphon androsaceus* Benth. complex has been troublesome because of remarkable morphological similarity among species. During the past 160 years, members of this complex have been classified in 4 different genera, and numerous specific and infraspecific names have been applied. Despite numerous treatments written by early taxonomists, analytical studies were not performed on these species until recently. We examined morphometric relationships among 1264 individuals from 51 populations, from the Central and South Coast Ranges. We focused on populations from San Francisco to Santa Barbara County because much of the variability in flower color occurs in this region, and color has been used by previous authors to distinguish species and subspecies. We investigated morphological variation using an array of multivariate analyses, including cluster analysis, principal components analysis, and discriminant analysis. Our analyses show six species of the *L. androsaceus* complex occur in this region of California: *L. acicularis* (Greene) Jeps., *L. androsaceus, L. bicolor* Nutt., *L. croceus* (Eastw.) J. M. Porter & L. A. Johnson, *L. parviflorus* Benth., and *L. rosaceus. Leptosiphon croceus* and *L. rosaceus* were described nearly 100 years ago, but have not been included in recent treatments. Our results offer strong support for recognition of *L. croceus* and *L. rosaceus* at the species level.

The *Leptosiphon* (=*Linanthus*; see below) *androsaceus* group is a monophyletic lineage of Polemoniaceae (Bell and Patterson 2000) characterized morphologically within the genus by sessile flowers borne in terminal, bracteate heads, salverform corollas with long filiform tubes, and calyces with narrow intercostal hyaline membranes connecting the lobes. Although visited and presumably pollinated primarily by long-tongued flies, the species within the *L. androsaceus* complex exhibit a variety of breeding systems (Goodwillie 1997, 1999a, b).

Within the salverform-tubed leptosiphons, relative breadth of calyx membranes and lobes distinguishes two well marked groups (Table 1): the *L. androsaceus* group, characterized by membranes clearly narrower than the lobes, and the *L. ciliatus* group with membranes broader than the lobes. This distinction is also supported by molecular data (Bell and Patterson 2000). All are small, spring-blooming annuals occurring in grassland and woodland areas from the Sierra Nevada foothills to the Pacific Coast in western North America.

The remarkable morphological similarity among these species has hampered resolution of species limits and relationships. Furthermore, the nomenclature is extensive (Jepson 1943; Mason 1951; Munz 1959) and the task of sorting and assigning names is challenging. Hooker (1870) referred to *Linanthus* as "one of the most variable genera of hardy annuals, the limits between the species of which are as difficult to draw from living specimens as from herbarium ones." There are few morphological characters available to distinguish these similar species, and compounding the taxonomic confusion is the fact that these characters often exhibit a high degree of variability within a species. *Leptosiphon parviflorus,* for example, is an especially variable species with regard to corolla tube length and corolla color, two characteristics traditionally used to identify species.

Taxonomic background. In his monograph of Polemoniaceae, Grant (1959) recognized 6 sections of *Linanthus* based on several morphological features. Among these was his sect. *Leptosiphon.* The earliest recognized species in this section were described originally by Bentham (1833) as members of the genus *Leptosiphon.* Greene (1889–1892) combined several genera into a single genus, *Linanthus,* based largely on the presence of opposite, palmately lobed leaves. Grant's (1959) sections largely represent the genera that were combined into *Linanthus* by Greene. Porter and Johnson (2000) presented a revision of the entire family with the goal of recognizing only monophyletic groups. Their revision, supported by morphological and molecular data (Johnson et al. 1996; Porter 1996; Bell et al. 1999; Bell and Patterson 2000) divides *Linanthus sensu* Greene into two distinct, non-sister genera, *Linanthus* and *Leptosiphon;* the latter genus includes, but is not limited to, all of the *L. androsaceus* group. We follow Porter and Johnson's taxonomy in this paper (Table 1).

Although many treatments involving the *L. androsaceus* group have been provided by earlier taxonomists (Bentham 1833, 1845, 1849; Endlicher 1836–1840; Nuttall 1848; Bentham and Hooker 1876; Gray 1870, 1886; Greene 1889–1892; Jepson 1901, 1925, 1943; Danforth 1945; Mason 1951), no

TABLE 1. TAXONOMY OF LONG-TUBED *LEPTOSIPHON.*

L. ciliatus group—calyx membranes wider than calyx lobes

L. breviculus (A. Gray) J. M. Porter & L. A. Johnson
L. ciliatus (Benth.) Jeps.
L. montanus (Greene) J. M. Porter & L. A. Johnson
L. nudatus (Greene) J. M. Porter & L. A. Johnson
L. oblanceolatus (Brand) J. M. Porter & L. A. Johnson

L. androsaceus group—calyx membranes narrower than calyx lobes

L. acicularis (Greene) Jeps.
L. androsaceus Benth.
L. bicolor Nutt.
L. croceus (Eastw.) J. M. Porter & L. A. Johnson
L. jepsonii (Schemske and Goodwillie) J. M. Porter & L. A. Johnson
L. latisectus (E. G. Buxton) J. M. Porter & L. A. Johnson
L. minimus (H. Mason) R. Battaglia
L. parviflorus Benth.
L. rosaceus (Greene) R. Battaglia
L. serrulatus (Greene) J. M. Porter & L. A. Johnson
unidentified populations
   MRM   Morgan Meadow, Santa Cruz Co.
   PIN   Pinnacles National Monument, San Benito Co.

analytical studies have been performed. The first explicit analyses include two recent morphometric studies that sampled populations in northern California where the distribution ranges of these taxa overlap (Buxton 1993; Schemske and Goodwille 1996). Each of these studies revealed the presence of previously unrecognized taxa and provided statistical support for the recognition of the other members of this complex. Nevertheless, these studies sampled only a fragment of the variation present in the entire complex.

Only through quantitative data analyses can species limits within the complex be resolved. Determination of species limits is a prerequisite for understanding phylogenetic relationships among members of this group. Our study continues to clarify taxonomic relationships in the *L. androsaceus* complex by sampling from populations in the southern portions of its range. In order to determine which taxa occur in this geographic area, we used a number of multivariate analyses (PCA, Cluster, DA) to group specimens based on morphological similarities. We were specifically interested in determining whether any of the various *L. parviflorus* color morphs merited taxonomic recognition. Once the taxonomic groups were identified, we used PCA and DA analyses to identify the morphological characteristics most responsible for distinguishing the taxa.

METHODS

Sampling. Quantitative morphological data for this study were gathered from fresh specimens collected during spring of 1997 and 1998. We collect-

ed 1264 samples (individual plants) from 51 populations from San Francisco to Santa Barbara County (Table 2; Fig. 1). This is the region in which *L. parviflorus,* a particularly troublesome taxon, exhibits the greatest variation in color and color pattern.

In addition, plants were grown in the greenhouse from field-collected seed to estimate whether observed character differences were influenced by environmental conditions. Cotyledon measurements were also made on these plants.

Characters. We obtained a range of leaf and floral measurements and observations to represent the overall form of the plant (Table 3). A total of 44 measurements was taken on each specimen. Many of these characters have been used to distinguish among species in this complex. To ensure that measurements were comparable, specimens for measurements were prepared as follows: From each plant, one leaf and one flower were mounted on an overhead transparency using clear packing tape. The first leaf below the inflorescence was chosen to represent the leaves of the plant. The calyx and corolla were dissected prior to being examined. The calyx was cut between the lobes to flatten it and obtain a clear image. The corolla was dissected by peeling three or four of the limb lobes, including the throat, from the tube and mounting them independently. The stigmas and style were removed and mounted.

Measurement. Qualitative characters, counts, and two length measurements were scored by hand prior to mounting specimens. Schemske and Goodwillie (1996) showed patterns of calyx pubescence in this group fall into two categories; fewer than 100 or greater than 100 trichomes per lobe. We counted the number of trichomes per calyx lobe if they numbered fewer than 100.

The remaining continuous characters were measured by digitizing the contours of the mounted specimens using a computerized image capturing system. We used the software program MorphoSys ver. 1.26 (Meacham and Duncan 1989), which allows the contour of a specimen to be drawn, landmarks selected, and data saved. This allowed for a relatively rapid and accurate means of collecting the large amount of data necessary for a morphometric analysis. Width measurements for the corolla and leaf lobes were spaced proportionally throughout the proximal region of the lobe, at 0.5, 0.7, 0.8, and 0.9 of the total length of the lobe, because this region appeared to be the most variable.

Analytical techniques. We used several multivariate methods per Pimentel's (1993) recommendation. If the results of several different analyses agree, then violations of assumptions such as nonlinearity and heteroscedacity are minimized and the results of the analyses are robust. The multivariate statistical methods we used included: Cluster Anal-

TABLE 2. COLLECTION LOCALITIES OF *LEPTOSIPHON* SAMPLES. All collections were made in 1998 except EDG, MPT, MTH, PIN, RSA, and WSK, which were made in 1997. See Table 4 for color code translation.

Acronym	Location	Number sampled (N)	Color code
L. acicularis			
BFX	Bolinas Fairfax Rd., Marin Co.	14	9
PLR	Pleasanton Ridge Regional Park, Alameda Co.	25	9
SNB	Sinbad Canyon, Pleasanton Ridge Regional Park, Alameda Co.	25	9
L. androsaceus			
AQS	Almaden Quicksilver County Park, Santa Clara Co.	25	10
BFR	Bolinas Fairfax Rd., Marin Co.	25	10
BNK	Bunker Hill, Highway 280, San Mateo Co.	25	10
DUN	East Dunne Rd., Santa Clara Co.	25	10
JPR	Jasper Ridge Biological Preserve, San Mateo Co.	25	10
LMP	Reynolds Rd., Stanton Ranch, Santa Clara Co.	25	10
MHM	Eastern side of Mount Hamilton, Santa Clara Co.	25	10
MIN	Mines Rd., Alameda Co.	25	10
MTD	Mount Diablo State Park, Contra Costa Co.	25	10
MTH	Mt. Hamilton, Santa Clara Co.	24	10
RSA	Rancho San Antonio County Park, Santa Clara Co.	15	10
RSN	Rancho San Antonio County Park, Santa Clara Co.	25	10
UVA	Uvas Rd., Santa Clara Co.	25	10
L. bicolor			
ADL	Paso Robles, San Luis Obispo Co.	25	11
CHI	Red Hill Rd., Chinese Camp, Tuolumne Co.	25	3
COL	Coalinga Road, Monterey Co.	25	11
DPC	Del Puerto Canyon Rd., Santa Clara Co.	25	3
PRB	Parkfield, Monterey Co.	25	11
RDH	Red Hill Rd., Chinese Camp, Tuolumne Co.	25	11
STR	Reynolds Rd., Stanton Ranch, Santa Clara Co.	25	11
VNY	Vineyard Canyon Rd., Monterey Co.	25	3
WSK	Whiskey Falls, Madera Co.	22	11
L. croceus			
MSB	Moss Beach, San Mateo Co.	25	8
L. latisectus			
CUT	Potter Valley, Mendocino Co.	25	11
EEL	Potter Valley, Mendocino Co.	25	11
P. parviflorus			
ALQ	Almaden Quicksilver County Park, Santa Clara Co.	25	1
CAC	Cachagua Rd., Monterey Co.	25	1
CLG	Coalinga Rd., Monterey Co.	25	3
CRZ	Highway 58, San Luis Obispo Co.	25	2
CVR	Carmel Valley Road, Monterey Co.	25	2
DLP	Del Puerto Canyon Rd., Santa Clara Co.	25	3
DNN	East Dunne Rd., Santa Clara Co.	25	1
EDG	Edgewood County Park, San Mateo Co.	24	1
EGW	Edgewood County Park, San Mateo Co.	25	1
EHT	Carmel Valley Road, Monterey Co.	25	2
FGM	Figueroa Mountain Rd., Santa Barbara Co.	25	2
FGS	Happy Canyon Rd., Santa Barbara Co.	25	2
FIG	Figueroa Mountain Rd., Santa Barbara Co.	25	2
FTO	Impossible Canyon, Fort Ord, Monterey Co.	25	6
HST	Hastings Natural History Reservation, Monterey Co.	25	4
JSP	Jasper Ridge Biological Preserve, San Mateo Co.	25	1
JSR	Jasper Ridge Biological Preserve, San Mateo Co.	25	5
LPD	Los Padres National Forest, San Luis Obispo Co.	25	6
LCU	Lucile's Court, Boulder Creek, Santa Cruz Co.	25	8
PKS	Parkfield, Monterey Co.	25	2
PNC	Pinnacles National Monument, San Benito Co.	25	3
PRK	Parkfield, Monterey Co.	25	6
QHL	Quail Hollow Ranch County Park, Santa Cruz Co.	25	7

TABLE 2.   CONTINUED

Acronym	Location	Number sampled (N)	Color code
SAZ	Near Sierra Azul County Park, Santa Clara Co.	25	1
SND	Sandhill Rd., Santa Cruz Co.	25	2
TRK	Turkey Flat Campground, San Luis Obispo Co.	25	6
L. rosaceus			
MPT	Mori Point, San Mateo Co.	24	3
MRI	Mori Point, San Mateo Co.	25	3
unidentified			
MRM	Morgan Meadow, Santa Cruz Co.	25	10
PIN	Pinnacles National Monument, San Benito Co.	9	2
PNN	Pinnacles National Monument, San Benito Co.	25	2

ysis of a dissimilarity matrix (UPGMA), Principal Components Analysis (PCA) using a correlation matrix of the standardized data sets, and Discriminant Analysis (DA) on a variance-covariance matrix.

Several data matrices were used in our analyses. A summary of each data matrix with regard to identity, number of groups, number of specimens, and number of variables is shown in Table 4. Matrices 1, 2, and 2a were used to determine how many taxa (species) occured in the study region. Matrix 1 contains all data collected from field specimens during spring and summer 1998, and was used for screen-

ing variables to be included in the final analyses. Matrix 2 is a subset of Matrix 1 resulting from data evaluation, and containing representative samples from all species in the *L. androsaceus* complex except for *L. jepsonii, L. minimus* and *L. serrulatus* (Greene) J. M. Porter & L. A. Johnson comb. nov. These species do not occur in the geographical range covered by this study.

Matrices 3 and 4 were used to evaluate whether *L. parviflorus* color morphs merited infraspecific recognition. Matrix 3 is a subset of Matrix 1, containing representative samples from only populations identified as *L. parviflorus* and the *L. croceus* population from Moss Beach (MSB). *Leptosiphon croceus* was included in this data set to assess its relationship to *L. parviflorus*. It is the final data set for *L. parviflorus* resulting from data evaluation. Matrix 4 contains only populations identified as *L. parviflorus,* and was used to determine whether any of the various color morphs deserved taxonomic recognition.

Data evaluation. Multivariate techniques require a rigorous examination of data, because the effects of an ill-conditioned data set can be compounded across several variables and have quite substantial effects (Tabachnick and Fidell 1996). To minimize these risks, data from Matrix 1 were screened for accuracy, precision, missing data, and co-linearity. Several qualitative variables were excluded due to either difficulty in consistent interpretation of character ranks or a high degree of variability observed within a single population. These include calyx trichome length, corolla tube pubescence and glandularity, corolla throat pubescence, leaf pubescence and glandularity, degree of branching, conivent versus spreading stamens, number of bracts, number of internodes, and number of open flowers.

Because corolla color and color pattern were consistent within populations, the variables for tube, abaxial lobe, adaxial lobe, and throat ring color were summarized into one variable describing the 11 different color morphs (Table 5) observed in this study. These data were used only in the anal-
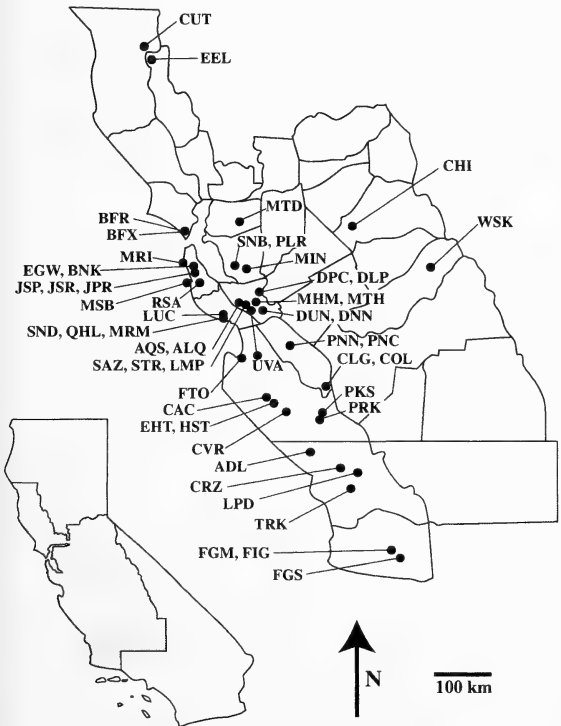

FIG. 1.   Location of *Leptosiphon* samples included in this study.

TABLE 3. MORPHOLOGICAL CHARACTERS ANALYZED. All distance measurements are in mm.

	Qualitative	MorphoSys	Hand-scored	Used in multivariate analysis
Calyx:				
Length of lobes		X		X
Total length of calyx		X		X
Width of calyx lobe:				
at 0.5 length of lobe		X		X
at base of lobe		X		X
Location of calyx pubescence (absent/ciliate/throughout)	X		X	
Degree of calyx pubescence (# trichomes/lobe)			X	Matrix 2
Length of calyx trichomes (short/medium/long)	X		X	
Glandular/not glandular	X		X	
Corolla:				
Length of corolla lobe		X		X
Width of corolla lobe:				
at base		X		
at 1/10 from lobe base				
at 5/10 from lobe base		X		X
at 7/10 from lobe base		X		
at 8/10 from lobe base		X		
at 9/10 from lobe base		X		X
Length of throat		X		X
Length of tube		X		X
Width of tube		X		X
Tube color	X		X	
Tube pubescence (absent/sparse/dense)	X		X	
Tube trichomes glandular/not glandular	X		X	
Throat trichomes present/absent	X		X	
Lobe color:				
Abaxial surface	X		X	
Adaxial surface	X		X	
Throat ring color	X		X	
Androecium and gynoecium:				
Length of filament		X	X	
Length of stigma			X	Matrix 2
Length of style			X	
Leaf:				
Length of palm		X		X
Width of palm		X		X
Length of middle lobe		X		X
Width of middle lobe:				
at base of lobe		X		X
at ½ from lobe base		X		X
at ¼ from lobe base		X		Matrix 3 & 4
at ⅛ from lobe base		X		X
Number of lobes per leaf			X	X
Pubescence (absent/ciliate/throughout)	X		X	
Glandularity (present/absent)	X		X	
General:				
Number of internodes on longest stem			X	
Number of open flowers per inflorescence			X	
Number of bracts subtending inflorescence			X	
Branching (none/above/below/throughout)	X		X	
Stamens connivent/spreading	X		X	
Total height of plant			X	X

TABLE 4. Data Matrices Used in Analyses. The number of groups refers to the number of groups used for multivariate analyses. Matrices 5–8 were not used in the multivariate analyses.

Data matrix	Description	Groups in analysis	Populations represented	Number of specimens	Number of variables
Matrix 1	All 1998 field data	53	53	1314	44
Matrix 2	Results of data analysis, all species included	51 (DA2-1) 9 (DA2-2)	51	1264	21
Matrix 2a	Variable means for each population in Matrix 2	1	51	51	21
Matrix 3	Results of data analysis, only *L. croceus* and *L. parviflorus* populations included	26	26	650	20
Matrix 3a	Variable means for each population in Matrix 3	1	26	26	20
Matrix 4	Results of data analysis, only *L. parviflorus* populations included	25 (DA4-1) 7 (DA4-2)	25	625	20
Matrix 5	All field data from 1997	N/A	6	118	29
Matrix 6	1997 Greenhouse data	N/A	3	72	26
Matrix 7	1998 Greenhouse data	N/A	19	276	26
Matrix 8	Cotyledon data from 1998 greenhouse plants	N/A	19	447	2

ysis involving populations of *L. parviflorus*. Most species in the *L. androsaceus* complex have two color morphs: white, and either pink, lavender, or yellow. *Leptosiphon parviflorus* is unique in that all the above color morphs occur. In addition, throat color varies, and markings on the limb lobes may be present (Fig. 2). Eight different color morphs of *L. parviflorus* were observed in this study.

Measurements taken using MorphoSys were first checked for precision (repeatability) by randomly choosing one population and remeasuring for each variable. Measurements that showed significant differences (P > 0.05) between measurement sessions were eliminated from our analysis.

The remaining 27 variables (23 metric continuous, two metric counts, one multistate, and one binary) were then checked for near-perfect correlation to reduce the risk of co-linearity. Multi-co-linearity problems occur when r > 0.9 (Tabachnick and Fidell 1996); therefore we eliminated selected variables from pairs with Pearson's correlation scores of r > 0.9.

Calyx pubescence and glandularity posed problems with data scoring. Degree of calyx pubescence could be measured as number of trichomes per lobe, but the trichome location and glandularity had to be coded (multistate and binary respectively). However, all three characters were highly correlated (all r values > 0.92), thus the two coded variables were omitted.

Style exsertion has been used in the past (Bentham 1833; Greene 1889–1892; Mason 1951; Munz 1959; Buxton 1993) to aid in characterizing members of this complex. We observed that style length, and therefore style exsertion, increased with age of the flower in *L. parviflorus*. In addition, tube length and style length were highly correlated, r = 0.944. Despite its previous taxonomic use, we excluded style length from our analysis.

Statistics. Cluster analysis was used to suggest similarity among populations. Results from the cluster analyses allowed us to define groups in later analyses that require group identity. Population

TABLE 5. Corolla Color Patterns Recorded in the *Leptosiphon androsaceus* Complex.

| Color code	Lobe color	Throat color	Additional markings
1	white	yellow	2 red spots at base of lobes ("two-spot")
2	white and/or lavender-pink	violet or yellow	striations on lobes ("candystripe")
3	white	yellow	
4	white	violet	
5	pink	yellow	2 red spots at base of lobes ("two-spot")
6	white	orange	1 red bar at base of lobes ("bullseye")
7	deep yellow-orange	orange	
8	deep yellow-orange	orange	2 red spots at base of lobes ("two-spot")
9	light buttery yellow	light yellow	
10	white or lavender-blue	violet at base, yellow distally	
11	pink	yellow with white ring distally	
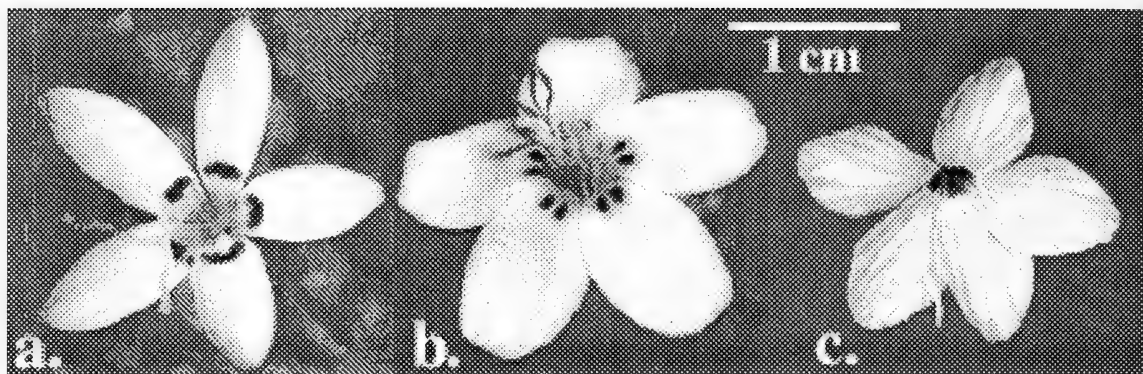
FIG. 2. Examples of the various corolla markings observed in *L. parviflorus:* a) "bullseye", red crescent shaped bar at base of lobe, b) "2-spot", two red spots at base of lobe, c) "candystripe", lavender striations on lobe.

means (group centroids) for each variable in Matrix 2 and Matrix 3 were calculated. New data matrices (Matrix 2a and Matrix 3a) were created using variable means for each population, and each was subjected to cluster analysis. The group average method for linkage (UPGMA) using a dissimilarity matrix generated by Euclidean distances was used (Sneath and Sokal 1973).

Principal components analysis (PCA) was primarily used to analyze the variables on a correlation matrix of the data sets Matrix 2 and Matrix 3. Data were standardized prior to the analysis as part of the SPSS (SPSS 1997) protocol for the PCA method.

Discriminant analysis (DA) was performed on a variance-covariance matrix of the Matrix 2 and Matrix 4 data sets. Discriminant analyses were run on the two data sets using several a priori grouping arrangements. Three analyses (DA2-1, DA2-2, DA2-3) were run on Matrix 2. DA2-1 used the 51 collection populations as predefined groups. DA2-2 used the results from the UPGMA and PCA analyses to assign individuals to the following groups: PNN, MRM, *L. androsaceus, L. acicularis, L. bicolor, L. latisectus, L. parviflorus, L. croceus,* and *L. rosaceus.* Because the sizes of the groups in DA2-2 were not equal (ranging from 25 to 625 individuals per group), the analysis was repeated using equal group sizes. DA2-3 used a subset of 25 individuals selected randomly from each group used in DA2-2. The Matrix 4 data set was subjected to two DA analyses, DA4-1 and DA4-2. A priori groups were defined by color morphology and based on the results from the PCA and cluster analyses: "2-spot" (all corolla colors), "bullseye," "candystripe," "yellow," "white with violet," and "white with yellow." The sizes of the groups based on color morphology were not equal, ranging from 25 to 200 individuals. The same reduction procedure was performed by randomly selecting 25 individuals from each group, and the analysis was run again (DA4-2).

RESULTS

Because of their large size, matrices generated (correlation, component, structure) and Geisser classification summaries are not included in this paper, but are in Battaglia (1999) or are available from the first author upon request. Results of analyses using all species are discussed first, results from the *L. parviflorus* color morph analyses are discussed second. Four of the 51 populations (MRI, MSB, PNN, MRM) were not identifiable using the current taxonomy (Patterson 1993; Buxton 1994; Schemske and Goodwillie 1996). Two of these were later identified as *L. croceus* (MSB) and *L. rosaceus* (MRI), species synonymized with *L. parviflorus* and *L. androsaceus* respectively. The PNN and MRM populations remained unidentifiable.

Cluster analysis—all species. The UPGMA cluster analysis of Matrix 2a (Fig. 3) is in general accord with the conventional taxonomy of the group, with several noteworthy exceptions. Five of seven species cluster together; however, *L. acicularis* and *L. parviflorus* do not.

Principal components analysis—all species. Results of PCA on Matrix 2 showed the total variance was generally well spread among variables, with only 77% of the total variance explained by the first 6 components. This indicates variables were generally independent of each other, with little correlation or covariation. Graphical representation of regression factor scores for each individual (not shown) indicate seven distinct clusters representing *L. acicularis, L. androsaceus, L. rosaceus, L. croceus, L. parviflorus, L. latisectus,* and *L. bicolor.*

Results from the component matrix indicate there was no single variable contributing to the observed variation among groups. More interestingly, corolla tube length had component scores of 0.232, −0.008, and 0.203 for the first three components. This indicates corolla tube length explained little of the observed variation. Although corolla tube length is traditionally used as a character to distin-
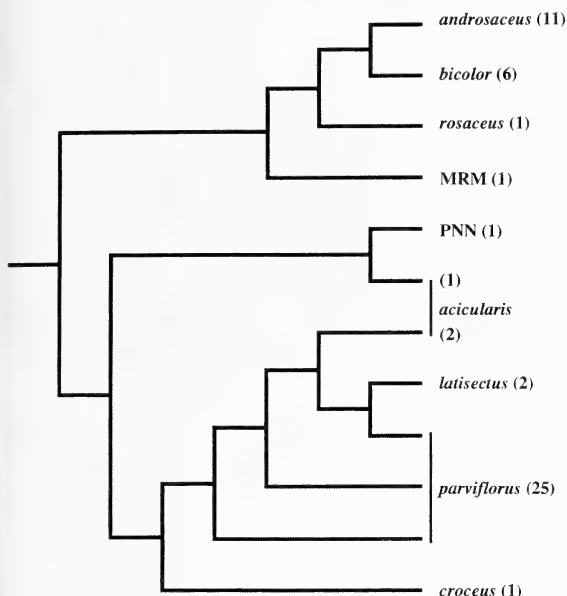
FIG. 3. Dendrogram of UPGMA cluster analysis for all species (Matrix 2a). MRM (Morgan Meadow) and PNN (Pinnacles) are two unidentifiable populations. Numbers in parentheses refer to the number of populations represented by the branch.

guish among species in this complex, it does not correlate with segregation on the first three components.

Discriminant function analysis—all species. (DA2-1). When using a priori groups based on the 51 collection sites, all Wilks' Λ values were small (0.040–0.575), indicating strong differences among group centroids for each variable. ANOVA's show significant differences (P < 0.001) among all variable means for each of the 51 populations.

Results of the Geisser classification summary for the 51 collection sites indicate three populations have 100% classification success: MSB (*L. croceus*), CHI (*L. bicolor*), and LUC (*L. parviflorus*). Ten populations have greater than 90% classification success: AQS, RSN, UVA (*L. androsaceus*), COL, STR (*L. bicolor*), CLG, JSR, QHL (*L. parviflorus*), MRI (*L. rosaceus*), and PNN (undetermined). One group, TRK (*L. parviflorus*), has a low score of 54%, and the remaining groups range from 64–88%. Of the 1264 individuals, 1053 (83.3%) were classified correctly based on collection site, indicating that all groups are unique.

Misallocations to collection sites in geographical proximity occurred frequently. In nearly every case, misallocations were within species groups that resulted from the UPGMA and PCA analyses. The exceptions involve three of the four unusual populations identified in the previous analyses. MRI (*L. rosaceus*) had 24 correct hits and 1 misallocation to BFR (*L. androsaceus*); PNN had 24 correct hits and 1 misallocation to ADL (*L. bicolor*); and MRM

had 16 correct hits, 4 incorrect classifications to JSR and CAC (*L. parviflorus*) and 5 misallocations to RSN (*L. androsaceus*). The unusual population from MRM was the only one to have members classified into two other species groups.

Results from DA2-3 (a priori groups of equal numbers defined by UPGMA and PCA, respectively) appear below. We do not discuss in detail results from DA2-2 because general patterns regarding group discrimination were the same, and graphical interpretation in two dimensions is complicated with the larger sample size. In each case one-way ANOVAS indicated variable means for all groups differed significantly (P < 0.001).

The first three canonical functions contained 74.4% of the variation in DA2-3, and the variance was evenly distributed among the functions. The first function in DA2-3 contained 33.3% of the variation. Strong group differences for all variables in DA2-3 was indicated by generally low Wilks' Λ scores (0.168–0.674). The majority of variables scored lower than 0.5.

Patterns are revealed by graphing the first two canonical discriminant functions (Fig. 4). Group separation is distinct: *L. croceus* and *L. rosaceus* are clearly separated from *L. parviflorus* and *L. androsaceus* respectively, *L. bicolor* and PNN are not separated, and MRM is closely associated with *L. androsaceus,* although individuals are still scattered between *L. parviflorus* and *L. androsaceus.*

A three-dimensional depiction (Fig. 5) of the first three discriminant function scores for individuals in DA2-3 reveals 7 distinct clusters, each corresponding to one of the 7 species. Individuals from the PNN and MRM populations do not form coherent groups.

Geisser classification results for each analysis are similar. In DA2-2 all but MRM (76%) have above 90% successful predicted group membership. In DA2-3, all but *L. androsaceus* (94%) have 100% successful classification.

Cluster analysis—L. parviflorus color morphs. We performed a UPGMA cluster analysis on the Matrix 3a data set to evaluate support for grouping *L. parviflorus* populations based on corolla color pattern (Fig. 6). *Leptosiphon croceus* (MSB) is clearly separated from *L. parviflorus.* Within *L. parviflorus,* all but one of these populations displaying two spots at the base of the petal lobe cluster together. Three populations with the "bullseye" pattern form a cluster, but this cluster and the excluded population LPD are nested deeply within the remaining populations of *L. parviflorus.* No other color morphs form discrete clusters.

Discriminant analysis—L. parviflorus color morphs. We performed a DA on the Matrix 3a data set. Based on the results of the previous analyses, all of the "2-spot" color morphs (white or pink) were grouped together for this analysis. The results from DA4-1 and DA4-2 were nearly identical, in-
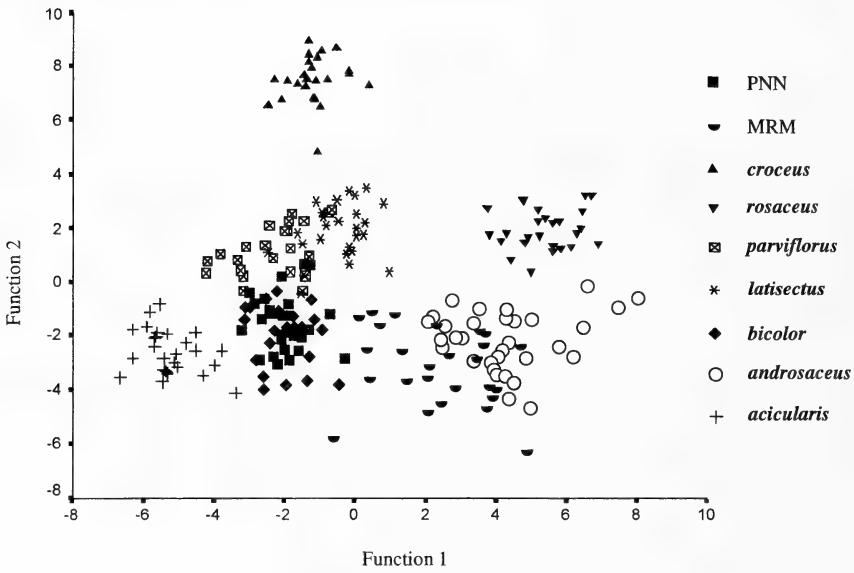
FIG. 4. Discriminant analysis results from all species (Matrix 2), equal group sizes (DA2-3). Graph of first two canonical functions for each individual.

dicating the unequal group sizes within DA4-1 did not adversely affect the analysis. Only the results from DA4-1 (all *L. parviflorus* individuals) will be discussed.

Wilks' Λ values for the variables were mostly greater than 0.8, demonstrating weak differences among group centroids for each variable; however, ANOVAS revealed that variable means for all groups were significantly different (P < 0.001). Tube length was the only variable for which there

was a strong group difference (Wilks' Λ = 0.385). The three petal lobe measurements (tube width, plant height, and leaf mid-lobe width) had Wilks' Λ scores ranging from 0.518 to 0.673.

Geisser classification showed that "candystripe" morphs had the lowest predicted group membership scores, with 71% being classified correctly. Misallocations for this color morph were made to each other color group, with the greatest number (25) being classified into the "white with violet" group.

+ *acicularis*   × *latisectus*
■ *androsaceus*   ◆ *parviflorus*
◇ *bicolor*   ▼ *rosaceus*
▲ *croceus*   ○ MRM
         □ PNN
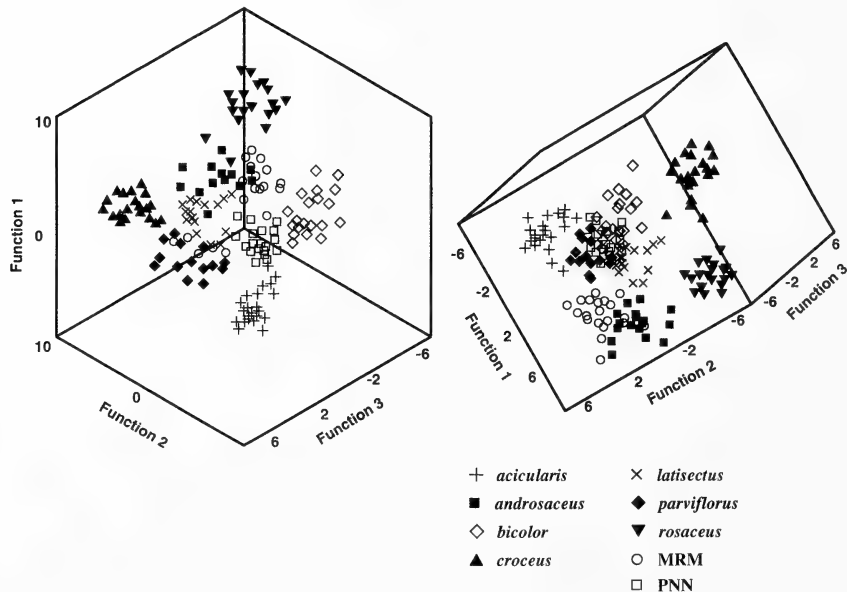
FIG. 5. Discriminant analysis results from all species (Matrix 2), equal group sizes (DA2-3). a) Three dimensional graph of the first three discriminant scores for each individual. b) Same graph with axes rotated.
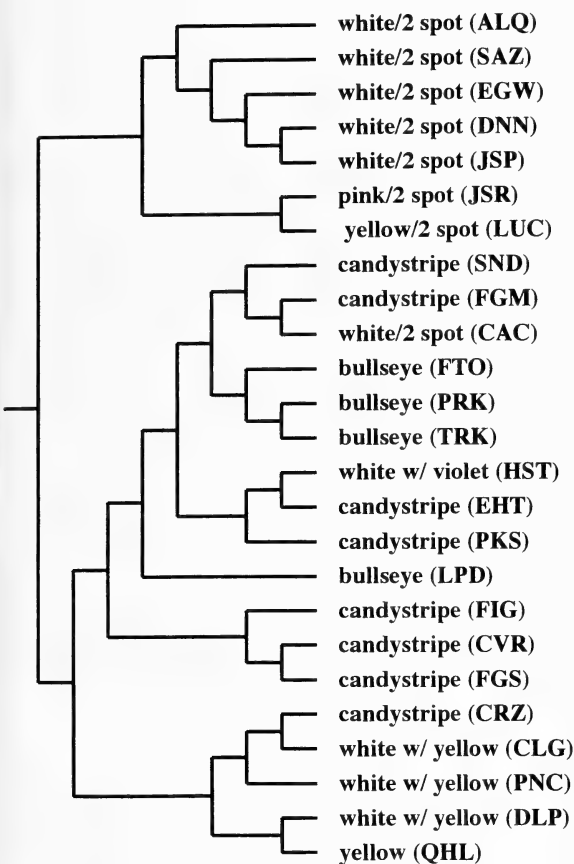
FIG. 6. Dendrogram of UPGMA cluster analysis for *L. parviflorus* color morphs (Matrix 3a). Acronyms refer to population locations.

The "white with violet" flowers were allocated correctly 92% of the time; however these specimens came from one population, and the two misclassified individuals were allocated to the "candystripe" group.

The "2-spot" morphs had 87.5% correct classification, which was lower than expected based on results from PCA but consistent with prior PCA and cluster analyses. Of 200 specimens, 175 were classified correctly and 25 were misallocated to each of the other color morphs. Case-wise examination of these 25 misallocations showed 22 were from the CAC population, the same population that did not cluster with other "2-spot" populations in the cluster analysis. Taking this into consideration, the remaining individuals of the "2-spot" morph show 98% correct classification.

The "white with yellow" and the "yellow" morphs had high classification rates, 97.3% and 100% respectively. The two misallocations of the "white with yellow" morph were to the "yellow group," a single population. The "white with yellow" morph shows general affinity for the "yellow" morph based on misallocations, but with 100% classification of "yellow," affinities of "yellow" with other morphs cannot be assessed.

The correctly predicted group membership for "bullseye" was 86%, but no affinities to other groups could be determined because misclassified individuals were allocated to each of the other color morphs. In addition, misallocations did not share similar patterns observed in the PCA and cluster analyses. In the UPGMA tree, FTO, TRK, and PRK clustered together, while LPD was excluded. Case-wise analysis of the misallocations revealed nine of 14 misallocations were from the FTO population, rather than the LPD population. Results from discriminant analysis are consistent with geographical distributions of these populations: FTO occurs near the coast while PRK, TRK and LPD are closer to each other in the inner Coast Ranges.

We extracted five canonical discriminant functions in our analysis; 93% of the total variation was explained in the first three axes (55.7%, 24.5%, and 12.8%, respectively). Corolla tube length and width scored high on the first axis (0.677 and 0.494). Corolla tube length is not particularly informative in distinguishing species in the Matrix 2 analyses, but it is important in distinguishing the "2-spot" *L. parviflorus* morphs from the remaining color morphs. Width of corolla lobe at the tip contributes most to the second axis, separating the narrower lobed "bullseye" morphs from the more rounded "white with yellow" morphs (Fig. 7).

Group differences based on individual variables. Results from the PCA and DA demonstrated that most variables were necessary for distinguishing among groups, whether they were groups based on species or color morphs of *L. parviflorus.* Discrimination among species was primarily based on calyx pubescence, corolla lobe length, corolla lobe width, and leaf lobe width. When only *L. parviflorus* populations were examined, PCA indicated most all variables were necessary for discrimination. On the other hand, DA showed corolla tube length and width, along with corolla lobe tip width, to be the most important variables in distinguishing the "2-spot" morphs from the remaining color morphs of *L. parviflorus.*

Greenhouse data. Nearly all measurements (means for each variable) from the plants grown in the greenhouse were larger than those collected from the field populations, but all variables fell within the range of measurements observed in the field populations. This indicates that there is a genetic basis for the observed differences, and environmental conditions do not greatly effect the variables used to distinguish among the various taxa.

The potential for cotyledon characters in helping to distinguish species of *Leptosiphon* should be of interest to students of the genus. We noticed important patterns in our analysis of cotyledon width and length measurements. There were two basic cotyledon morphologies: long and linear, versus
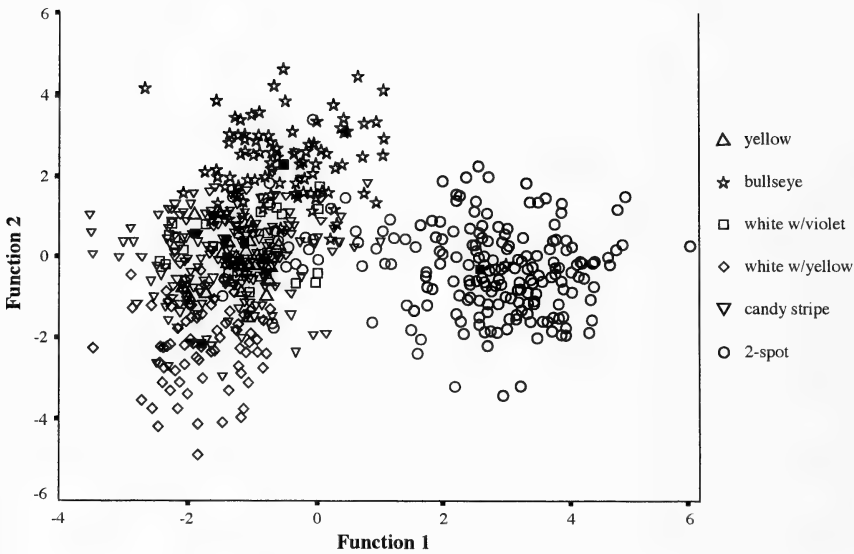
FIG. 7. Discriminant analysis from *L. parviflorus* color analysis (Matrix 3), all specimens (DA4-1). Graph of first two canonical functions for each individual.

shorter, rounded, and more or less obovate. The cotyledons of *L. acicularis* are linear and extremely long, with a length-to-width ratio of 7.1. *Leptosiphon parviflorus* also has linear cotyledons, with a ratio of 5.1; however two populations of *L. parviflorus* (LUC and JSP) had rounded cotyledons. These are each "2-spot" populations. The remaining species surveyed had oval to obovate cotyledons. *Leptosiphon androsaceus* had a length-to-width ratio of 1.8; *L. bicolor,* 1.9; *L. croceus,* 1.5, and *L. rosaceus,* 1.4. The length-to-width ratio of *L. latisectus* was 1.6.

The unidentifiable population, MRM, had cotyledons consistent with *L. androsaceus.* They were short and rounded, with a length-to-width ratio of 1.6. The cotyledons of the other unusual population, PNN, were longer and narrower than those of *L. bicolor* to which it was affiliated, with a ratio of 2.5, but they were not as linear as the cotyledons of *L. parviflorus.*

DISCUSSION

In closely related species that show far more similarities than differences, it is important to examine carefully all characters and to seek disjunctions among character states that may help define taxa and elucidate their relationships. Because the *L. androsaceus* group has a long taxonomic history accompanied by an abundance of nomenclatural activity, it is critical that we begin our analysis by examining morphological characters and identifying which of those best reflect relationships in the group. Despite the taxonomic age of the group, it has remained difficult to delineate species within it. Identification of taxa and the morphological characters that delimit them is a necessary precursor to

further research on evolutionary relationships among these species. We focused on morphological characters because they are the most practical means of identification and without proper identification, further systematic research is compromised. Our results should be used as a working hypothesis of the taxonomic structure within the group, providing a framework for future research on evolutionary relationships among its species.

Results from our analysis support recognition of six species in central California (*L. acicularis, L. androsaceus, L. bicolor, L. parviflorus, L. croceus,* and *L. rosaceus*) bringing the number of species within the *L. androsaceus* complex to nine (including *L. latisectus* and *L. jepsonii* from northern California, and *L. serrulatus* from the southern Sierra Nevada). *Leptosiphon croceus* and *L. rosaceus* were described nearly 100 years ago, but were synonomized with *L. parviflorus* and *L. androsaceus* by later authors (Milliken 1904; Jepson 1925). Neither author offered any explanation for their action; however, the omission of these species may be explained by several factors, including the morphological similarity among all members of this complex, the large amount of variation observed in the few characters used for distinguishing them, and the relative rarity of both species. Each is known from only a few populations collected from coastal bluffs in the San Francisco Bay region. These bluffs have undergone severe disturbance from increased developmental activities in the last hundred years, and it is likely that of the populations of these species that were known, few remain. For example, *L. croceus* was originally described from a population near Pt. San Pedro, in San Mateo Co. In her description of the species, Eastwood (1904) observed

that "it covered the ground for several acres . . . the great masses almost monopolized the ground." Despite its historical presence, *L. croceus* no longer occurs in the Pt. San Pedro area. Today only one population of *L. croceus* is known.

In addition to the 6 species mentioned above, this study also identified 2 unusual populations. One relatively invariable population, from Pinnacles National Monument (PNN), consists of plants that most closely resemble *L. bicolor,* but its limb and stigmas are somewhat larger and the calyx shorter than typical *L. bicolor.* The coloration is also unusual, being light lavender (darker on the margins of the lobes fading to white near the throat) instead of the typical white or pink. This population is particularly interesting because *L. bicolor* is generally the least morphologically variable species in the *L. androsaceus* complex. In addition to the morphological similarity of PNN to *L. bicolor* evidenced by the multivariate analyses, the PNN plants grown in the greenhouse readily set seed, indicating it is autogamous. The only other plants to set seed in the greenhouse were from populations of *L. bicolor.*

The other unusual populations is the highly variable population from the Santa Cruz Mountains (MRM), a mosaic of *L. parviflorus* and *L. androsaceus.* Limb size was smaller than *L. androsaceus* and more like that of *L. parviflorus.* Flower color and limb lobe shape were like the white form of *L. androsaceus* (white lobes with a throat that is violet at the base and yellow above). Calyx pubescence is a stable character, yet the calyces from this population ranged from completely glabrous, to ciliate, to densely pubescent throughout, although never glandular. The within-population variance for most characters was high.

Morphological relationships among the L. an-drosaceus *complex in the Central and South Coast Ranges.*

Leptosiphon acicularis. This species is most clearly defined from others in this complex by the long, narrow, nearly needle-like leaf lobes. The size of the leaf palm is also the smallest in the complex, thus the leaves appear to be very finely dissected. The length of the calyx is long (7–9 mm), with the calyx lobes being narrow and much longer than the fused portion. *Leptosiphon acicularis* most closely resembles *L. bicolor,* both of which are the smallest-flowered members in this group. The limb of *L. acicularis* is always yellow, but the short corolla tube may be yellow or a light tannish pink (i.e., not always yellow as cited by Patterson [1993]). The shape of the tube is reminiscent of *L. parviflorus,* being very thin (0.5 mm), but in contrast to *L. parviflorus,* which may have extremely long tubes, the tube of *L. acicularis* is the shortest in the complex (11–17 mm). Although the limb of *L. bicolor* may also be light yellow, it is clearly distinguished from *L. acicularis* by a suite of other characters (calyx

pubescence, shape of the leaf lobes, stigma length, stamen length).

Aside from its unique leaf morphology, *L. acicularis* also has a densely glandular pubescent calyx, whereas *L. bicolor* is pubescent only on the lobe margins and the trichomes are nonglandular. The size of the stamens and stigmas are also very different between the two species. *Leptosiphon acicularis* has some of the longer filaments in the complex (only those of *L. croceus* are as long), yet it has the one of the smallest limbs. Thus, the stamens of *L. acicularis* are well exserted, reaching ⅔ the length of the petal lobe. The stigmas are also large, being 2–4 mm long. The stamens of *L. bicolor* barely exceed the throat, and the stigmas are generally less than 1 mm long. As with most other species in this complex, the corollas open and close daily until senescence. The corollas of both species close for the night by mid-afternoon, earlier than the other species in the complex.

Leptosiphon androsaceus. This is the largest-flowered member of the *L. androsaceus* complex, and its floral characteristics most closely resemble *L. rosaceus* and *L. latisectus.* The limb lobes are the longest (8–11 mm) and differ from *L. rosaceus* and *L. latisectus* in being more oblong to oval, often with an apiculation at the tip. In comparison, the lobes of *L. rosaceus* and *L. latisectus* are very rounded. The limb is typically white or pale lavender, and the throat is commonly violet at the base, turning to yellow just as the throat flares into to limb. Buxton (1993) found populations in northern California with pink limbs, but none of the populations in this survey of central California had limbs with this color. The stigmas are generally long (2–4 mm) and the filaments are short in relation to the size of the limb. The corolla tube is typically moderate in length (19–26 mm), although this character is rather variable, and populations with longer tubes were observed. Similar to *L. rosaceus* and *L. latisectus,* the width of the tube is relatively wide (1 mm). Other characters differentiating this species include, leaf shape, plant height, calyx size, and most importantly calyx pubescent. The calyx is non-glandular and sparsely pubescent, with trichomes only on the margins of the lobes.

As with the other moderate- to short-tubed members, the total length of the calyx is moderately long (4–6 mm), with long calyx lobes relative to the fused portion. Nearly all leaf measurements for *L. androsaceus* are large for the complex. This species has the largest palm and longest middle lobe, although the width of the lobes is less than other species, giving it a less rounded appearance. The plants are typically the tallest growing members of the complex, and can occasionally be found growing on serpentine soil.

Grant (Grant and Grant 1965) observed a cyrtid fly, *Eulonchus smaragdinus,* visiting flowers of *L. androsaceus.* Although as a general rule he dis-

counted beetles as potential pollinators, we often observed beetles visiting flowers, probably not so much seeking out nectar as consuming pollen. Grant (Grant and Grant 1965) proposed *L. androsaceus* to be self-compatible and partially autogamous, with protandry being incomplete (overlapping stages). However, Goodwillie (1999b) showed it to be a self-incompatible, obligate outcrosser. Grant (Grant and Grant 1965) also suggested that *L. androsaceus* and *L. parviflorus* may hybridize locally, although he did not offer any evidence to support his statements. Hybridization is often invoked to explain unusual forms, but without careful study this explanation remains conjectural.

Leptosiphon bicolor. This species is morphologically the least variable member of the *L. androsaceus* complex. Its limb is small (3–4 mm), and its corolla tube is moderate in length (17–26 mm) and width (0.8 mm). It has by far the longest tube relative to the size of the limb. The limb is typically either pink or white with a yellow throat.

Its reproductive structures are small, with the stigmas 1 mm and stamens only one-half the length of the limb lobe, as might be expected in an autogamous species. The plants are relatively small (5–13 cm), and rarely is there more than one open flower per inflorescence. The flowers close by mid afternoon, opening again the following day.

The calyx is relatively long (7–9 mm), especially the length of the calyx lobes compared to the fused portion. The calyx is also ciliate and non-glandular, but, in contrast to *L. androsaceus* and *L. rosaceus,* the density of trichomes per lobe is generally greater in *L. bicolor* (30–50 trichomes per lobe). The leaves of *L. bicolor* are small, with short lobes and large palms. Buxton (1993) reported *L. bicolor* to have the greatest number of leaf lobes in the complex. In the southern populations, we found the variance of this character to be high both within and among populations, and we found no significant differences among the number of lobes in *L. bicolor, L. androsaceus, L. acicularis, L. parviflorus,* or *L. croceus.*

Goodwillie and Stiller (2001) recently elevated *Linanthus bicolor* (Nutt.) Greene subsp. *minimus* to species rank. While the scope of our study does not involve this species, following the taxonomy of Porter and Johnson (2000) the following combination is made:

Leptosiphon minimus (H. Mason) R. Battaglia, comb. nov. *Linanthus bicolor* var. *minimus* H. Mason. Madroño 9:249–255, 1948. *Linanthus minimus* Goodwillie and Stiller, Systematic Botany (2001). In press.

Leptosiphon croceus. First described by Eastwood (1904), *L. croceus* was later synonymized as varieties of *L. parviflorus* (Milliken 1904) and *L. androsaceus* (Jepson 1925). Our analysis supports its recognition as a distinct species. As with *L. la-*tisectus, *L. croceus* shares morphological characters with both *L. androsaceus* and *L. parviflorus* and many of the characters are intermediate between the two (e.g., limb size). Like *L. latisectus,* its leaf lobes are characteristically rounded at the tip, although its leaves are generally smaller. In addition, its leaves are thick and somewhat succulent. It is extremely low growing, being the shortest of all the species (2–6 cm). Although plants grown from seed of this population were slightly larger (6–8 cm) when raised in the greenhouse, they remained significantly shorter than any other species. Likewise, greenhouse grown plants also remained somewhat succulent, a likely response to conditions experienced directly on coastal bluffs. *Leptosiphon croceus* is often branched at the base with each branch having many closely spaced internodes. The close spacing of internodes makes the leaves appear "as if whorled" (Eastwood 1904). Its calyx is similar to that of *L. latisectus* in that the lobes and fused portion are nearly equal in length, and that it is densely glandular pubescent. The distinction lies in the size of the calyx and the width of the lobes.

Leptosiphon croceus has a much larger calyx (7–9 mm) than *L. latisectus,* and the width measurements are one-half to two times that of any other species. The limb is also similar in shape to that of *L. latisectus,* although the lobes are slightly larger (6–8 mm) and more rounded. The width of corolla lobes, both at middle and at the tip, are the largest in the complex. The corolla tube is also very long (29–37 mm), and thus distinguishes it from *L. latisectus.* The tube is generally much wider (0.9 mm) than that of *L. parviflorus,* more closely resembling *L. androsaceus* or *L. latisectus.* The limb is a bright, vibrant yellow, with an orange throat, and commonly has two red spots at the base of the lobes. The tube is yellow to yellowish-pink. In contrast to *L. latisectus,* the stigmas are relatively large (2–4 mm) and the filaments are long with the stamens exserted. The length of the filaments is similar to that of *L. acicularis.* Its cotyledons are rounded, like all the other species except *L. acicularis* and *L. parviflorus.*

Leptosiphon latisectus. This species has features of *L. androsaceus* and *L. parviflorus,* and closely resembles *L. croceus* in some features. As with *L. acicularis,* leaf measurements are important distinguishing characteristics. There are few leaf lobes, and they are wide at the tip, appearing more or less spatulate. Buxton (1993) showed palm lengths to be large, but variation in the two populations we sampled was too great to make conclusions. Its calyx is the smallest of any species in this group (5–7 mm). Its lobes are also small, nearly equal to the length of the fused portion. Its calyx is also densely glandular pubescent. Its limb shape and corolla tube width are similar to that of *L. croceus.* The limb lobes are moderate in size (5–7 mm), between *L. androsaceus* and *L. parviflorus,* but as with *L. croceus* they are especially wide at the tip, the lobes

being rounded to obovate. Unlike *L. croceus,* the tube is moderate in length (19–24 mm), similar to *L. androsaceus* and *L. bicolor.* The tube is also wide (≥ 1 mm) as is seen in *L. androsaceus* and *L. croceus.* A smaller limb with rounded lobes, a densely glandular calyx, and spatulate leaf lobes distinguish *L. latisectus* from *L. androsaceus,* while a comparatively larger limb, wider tube, and spatulate leaf lobes distinguish it from *L. parviflorus.* Corolla lobes are either dark pink or white, and the throat is yellow. The two pink populations sampled also had a white ring present at the top of the throat. Stigma length (1–2 mm) was among the smallest of any species (only *L. bicolor* had smaller stigmas), and filament length was short, barely exceeding the throat. Buxton (1993) suggested this might indicate possible autogamy, however Goodwillie (1999b) states *L. latisectus* is an obligate outcrosser. Individuals grown in the greenhouse had flowers that remained open even at night and in cooler temperatures, unlike any other species in the complex.

Leptosiphon rosaceus. This species was first recognized as *Leptosiphon parviflorus* var. *rosaceus* (Hooker 1870). Hooker considered this taxon a variety rather than a new species because he could find "no other difference" than the color and size of the flower (more than some authors would use). As to the flower, he stated it "was of a pale deep rose color, with a white or yellow eye" and that it "agrees with *L. androsaceus* one of the largest flowered of all," but that the lobes of the corolla had "a very different shape," being orbicular, versus narrower in *L. androsaceus* (Hooker 1870).

Greene (1889–1892) elevated Hooker's *Leptosiphon parviflorus* var. *rosaceus* to species level, *Linanthus rosaceus.* With regard to *L. rosaceus,* Greene observed that it was the "most beautiful plant of the *Leptosiphon* group" having stoutish short internodes, decumbent branches, obovate-spatulate leaf segments, the flower with a rose-red limb and an ample orange throat. He stated the "specific characters are as good as are found in this subgenus." He noted there was an albino form of this species as well. The population we observed during the course of this study was white. Another population discovered after the completion of the study was pink. Each of these observed populations had a yellow throat, not orange, as Greene described.

Occurring on coastal bluffs, its height and habit is similar to *L. croceus,* being densely branched and low growing (6–15 cm). It is significantly shorter than *L. androsaceus,* which is generally tall (17–31 cm) and not as densely branched. The leaf lobes of *L. rosaceus* are spatulate and more or less succulent. They are larger than those of *L. croceus* and even more rounded at the tip than either *L. croceus* or *L. latisectus.* The calyx is glabrous to sparsely pubescent, with the fewest number of trichomes per lobe than any other species in this complex (gen-

erally less than 10). If present, the trichomes are found only on the margins of the lobes and are non-glandular, another difference between it and both *L. latisectus* and *L. croceus.* The calyx lobes are moderately long (7–8 mm), but very wide at the base, appearing more or less deltoid.

The limb of *L. rosaceus* is moderate in size (7–9 mm) and similar in shape to *L. croceus* and *L. latisectus,* being smaller and more rounded than *L. androsaceus.* In contrast to *L. croceus,* the limb is white (or pink) with a pale yellow throat, and the corolla tube is not as long (21–26 mm). Tube length and width (1 mm) is more like that of *L. androsaceus* and *L. latisectus.* Unlike *L. androsaceus,* there is no violet coloration in the throat. The stigmas are generally long, being 4–5 mm, and well exserted beyond the throat.

Porter and Johnson (2000) did not include *L. rosaceus* in their recent revision; therefore the following new combination is made:

Leptosiphon rosaceus R. Battaglia, comb. nov.
  Leptosiphon parviflorus var. *rosaceus* Hooker. Curtis' Botanical Magazine 96, 1870. Tab 5863.

Leptosiphon parviflorus. Based on the analyses in this study *L. parviflorus* is taxonomically discrete at the species level, despite the observed variation. This species is variable in leaf and corolla size and shape, and especially so in corolla color pattern. In general, measurements for most morphological characters of *L. parviflorus* fell in the mid-range of the other species in the *L. androsaceus* complex (larger than *L. bicolor* or *L. acicularis,* smaller than *L. androsaceus* or *L. rosaceus*). The calyx is long (7–9 mm) and the calyx lobes are nearly equal in length to the fused portion. They are longer than *L. latisectus,* and not as wide as *L. croceus.* Like *L. latisectus* and *L. croceus,* an important identifying characteristic is its densely glandular pubescent calyx.

The limb lobes are 4–6 mm long and range from elliptic to oval or obovate. Lobe color may be white, pale yellow, yellow-orange, lavender-pink, or dark pink, with or without red spots or darker pink striations. The throat may be violet, yellow, or orange. In contrast to other species the throat is narrowly constricted at the base. Unlike *L. latisectus* or *L. croceus,* which have wider corolla tubes, the corolla tube of *L. parviflorus* is 0.6 (–1) mm, and 18–33 (–45) mm long. Tube length is highly variable, the standard deviation for tube length is twice that of the other species in this complex. Likewise, stigma length and style exsertion are also variable, as they lengthen over time in unfertilized flowers (Goodwillie 1999a). Stamens are well exserted, extending one-half the length of the corolla lobes. Goodwillie (1997) has shown *L. parviflorus* to be a self-incompatible, obligate outcrosser, with limited ability for wind pollination.

Corolla color patterns within L. parviflorus. Clearly different color patterns can be distinguished in this species, and some of these morphs correlate with other morphological features; however, the results of the multivariate analyses show distribution of these color patterns across *L. parviflorus* do not support sublevels of groupings. Within *L. parviflorus* the "2-spot" morph has the strongest support, and there is some weak support for the "bullseye" and "white with yellow" morphs based on the UPGMA clustering (Fig. 6) and the DA (Fig. 7), but examination of the variables fails to reveal distinct differences among the groups based on color.

Tube width and tube length are the characters responsible for the greatest separation between "2-spot" and the other color forms. The corolla tubes of the "2-spot" morph are generally very long (28–40 mm) and somewhat wider (0.8 mm) than those of the remaining color morphologies (0.5 mm). Tube length in the "bullseye" morph is also longer than average (22–29 mm), though not as long as the "2-spot," and, like the other color morphs, is much narrower (0.5 mm).

The limbs of "2-spot" and "bullseye" are also different, and provide a clearer separation than tube length. The "2-spot" color morphs have limb lobes that are larger than "bullseye" and are similar in shape to most other color morphs. In fact, all corolla measurements are consistently higher for the "2-spot" than the "bullseye" morphs. This is particularly true of the tip of the limb lobe, which is the largest in "2-spot" and the smallest in "bullseye." The limb lobes of "bullseye" are consequently narrower and more elliptic than the "2-spot," which are generally wider and more rounded, or flattened (Figure 2).

The differences between the "2-spot" and "bullseye" color morphs is interesting because these are the only color morphs with red markings on the corolla lobes. The presence of two red dots could seemingly evolve to become one large bar, or vice versa, and we would have expected their morphologies to be more similar. Also, the "2-spot" flowers have a yellow throat, whereas the "bullseye" have a dark yellow-orange throat.

Remaining Questions

Of the species in the *L. androsaceus* complex, *L. parviflorus* in particular raises many questions and merits further study. How is the variation in color pattern maintained? There is no geographic component to the color morphologies observed in our analysis, and only limited morphological separation. With such a highly modified corolla (nectar guides and long nectar tubes) and obligate outcrossing, it seems natural to expect specific pollinators are involved. Zebell (1993) examined a similar pattern of corolla color variation in *Calochortus venustus Benth.* He hypothesized that "flower color and pattern are 'released from tight pollinator se-lection pressures'. . . as long as enough flowers get pollinated to maintain the species." Perhaps the limited wind pollination in *L. parviflorus,* as reported by Goodwillie (1997), is enough of a selection release to allow for such variation in color morphology.

Based on the recent analytical work of Buxton (1993), Schemske and Goodwillie (1996), and Battaglia (1999), *L. parviflorus* should be approached with a careful eye. It is highly variable, not only in regard to color patterns, but in other vegetative and floral characters. Further taxonomic investigations, particularly populations of *L. parviflorus* from the Sierra Nevada foothills and south of the range covered in our analysis, are warranted to fully assess the variation observed in this species. Only after the fundamental morphological field work is completed to circumscribe the taxa can we begin to address other questions concerning phylogenies, population genetics, or the evolutionary history of the complex in California.

TAXONOMIC KEY TO THE *LEPTOSIPHON ANDROSACEUS* COMPLEX

1. Corolla tube <10 mm . . . . *L. serrulatus*
1.′ Corolla tube >10 mm.
   2. Calyx densely pubescent throughout, trichomes glandular or non glandular.
      3. Leaf and calyx lobes acerose, corolla lobes generally <4 mm, corolla lobes yellow. . . . .*L. acicularis*
      3.′ Leaf and calyx lobes not acerose, corolla lobe color variable.
         4. Corolla lobes <3 mm, tube <14 mm, northern Puget Sound, Vancouver Island, possibly Coastal N CA . . . . *L. minimus*
         4.′ Corolla lobes >3 mm.
            5. Calyx lobes deltoid, width at middle of lobe 1 mm, corolla lobes rounded at apex, always yellow, generally <7 cm tall, coastal bluffs San Mateo Co . . . . *L. croceus*
            5.′ Calyx lobes narrowly acute, width at middle of lobe <1 mm, corolla lobes not both rounded at apex and yellow, generally >7 cm tall.
               6. Corolla tube width generally >1 mm, leaf lobes commonly spatulate, >2 mm wide, corolla lobes generally >6 mm and rounded . . . . *L. latisectus*
               6.′ Corolla tube width generally <1 mm, leaf lobes not commonly spatulate, <2 mm wide, corolla lobe generally <6 mm and shape varied elliptic to obovate . . . . *L. parviflorus*
   2.′ Calyx not densely pubescent, trichomes ciliate and non glandular.
      7. Corolla lobes <4 mm long, stigmas <1 mm . . . . *L. bicolor*

7.′ Corolla lobes >4 m long, stigmas >1 mm
  8. Corolla lobes 4–6 mm long, stigmas
     generally <2 mm .... *L. jepsonii*
  8.′ Corolla lobe 6–14 mm long, stigmas
     generally >2 mm
     9. Leaf lobes spatulate and more or
        less fleshy, corolla lobes generally
        6–8 mm long and rounded, low
        growing, coastal San Francisco Bay
        area .... *L. rosaceus*
     9.′ Leaf lobes not as above, corolla
        lobes generally >8 mm long, often
        with an apiculation at tip ......
        .... *L. androsaceus*

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NOTEWORTHY COLLECTIONS

CALIFORNIA

CHORIZANTHE PARRYI VAR. *FERNANDINA* (POLYGONACEAE)—Ventura Co., S. slope of Laskey Mesa, Ahmanson Ranch; NE 3.2 Km Mureau Road and 101 Freeway, abandoned roadbed on compacted soils, San Andreas sandy loam, 1 May 1999, *R. E. Riefner & T. Bomkamp 99–271* (RSA); same location as above, 3 Jun 1999, *R. E. Riefner 99–283* (RSA); same location as above, 19 Jun 1999, *R. E. Riefner 99–299* (RSA).

Previous knowledge. Historically known from sandy places along drainages of the San Fernando Valley, northeastward into the Castaic Creek and Lake Elizabeth areas of the Liebre Mountains, and southward along the Los Angeles coastal plain into Orange County near Santa Ana (Reveal & Hardham 1989, Phytologia 66:98–198). Reveal and Hardham (loc. cit.) also report a J. G. Lemmon collection from San Bernardino County, but without other locality data, and several C. C. Parry collections without any locality information. Reveal and Hardham (loc. cit.) report 32 collections of the taxon, the most recent being

Hoffmann's 1929 specimen from Elizabeth Lake. To this may be added an undated A. Davidson collection (s.n.) from Toluca (RSA 392509), and another A. Davidson specimen (s.n.) dated 11 May 1890 from Burbank (RSA 392787), both in Los Angeles County. These two specimens bear Reveal's annotation labels and were apparently omitted inadvertently from the 1989 paper.

Significance. Widely thought extinct (e.g., Skinner & Pavlik, C.N.P.S. Inventory of Rare and Endangered Vascular Plants of California, 5th ed., 1994; Hickman, ed., The Jepson Manual: Higher Plans of California, University of California Press, 1993; Reveal & Hardham loc. cit.). The type locality is San Fernando Canyon, Los Angeles County. The Laskey Mesa population represents a first record for Ventura County, and at present, the only known extant population. Seed collected from a number of the stands comprising the Laskey Mesa population have been placed into long-term storage at Rancho Santa Ana Botanic Garden (M. Wall, personal communication).

—STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

MORPHOLOGICAL ASPECTS OF SEEDLING ESTABLISHMENT IN FOUR TEMPERATE REGION *PHORADENDRON* (VISCACEAE) SPECIES

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ABSTRACT

Morphological aspects of seedling establishment were studied in four species of the mistletoe genus, *Phoradendron* (Viscaceae). Marked differences occurred between species. In *P. densum* and *P. villosum* the plumular shoot developed as the main shoot of the plant, whereas in *P. juniperinum* the plumular shoot failed to develop in about 10% of seedlings. When the plumular shoot failed to develop a nonplumular seedling shoot displaced the original seedling axis to a lateral position near the base of the developing nonplumular shoot. The undeveloped seedling axis may remain attached and living for several years. In *P. californicum* the plumular shoot never developed in two of the populations studied, but did develop in a small percentage of individuals in a third population. In both species nonplumular shoots developed from a mass of tissue, termed the haustorial cushion, that forms immediately beneath the holdfast. A haustorial cushion was also observed in *P. densum,* but the shoot buds that formed on the cushion rarely developed into shoots. Cotyledon characters also varied between species, but in all four species the small cotyledons were persistent. Contrary to earlier reports, the cotyledons do not later develop into foliage leaves. In agreement with Kuijt (1990) we regard the cryptocotylar condition observed in *P. californicum* and, on rare occasion, in *P. juniperinum,* both squamate species, to be advanced. The morphological, ecological and evolutionary implications of these observations are illustrated and discussed.

Phoradendron and six closely related genera comprise the mistletoe family, Viscaceae. It has recently been suggested that the seven viscoid genera be transferred to the Santalaceae (APG 1998). The large genus *Phoradendron* is broadly divided into two subgroups, based on the presence or absence of scale-like appendages, the cataphylls (Wiens 1964). The acataphyllous species are predominantly northern in distribution, and all but one of the U.S. species are from this group. Monographs of the genus include those by Trelease (1916) and Wiens (1964) (acataphyllous species only). A revision of the entire genus is now in progress (Kuijt personal communication). Ashworth (2000) has analyzed phylogenetic relationships in the tribe Phoradendreae, which includes both *Phoradendron* and the sympatric and morphologically similar genus, *Dendrophthora.*

The seven viscacean genera are considered to have relatively uniform seedlings (Kuijt 1982), except for the genus *Arceuthobium.* Typically, the elongating root axis is the first organ to emerge from the seed (Calvin 1966; Kuijt 1969; Tubeuf 1923). As the tip of the root contacts the host branch, a disc-shaped holdfast is formed. Subsequently, the seedling becomes erect, with its cotyledons and shoot tip still enclosed within the fruit mass. Eventually the fruit vestiges are shed and the elongating plumular shoot emerges. Developed seedlings of both *Viscum album* L. (Tubeuf 1923)

and *Phoradendron macrophyllum* (Engelm.) Cockerell (Calvin 1966) have an elongate hypocotyl, two small cotyledons and a plumular shoot. While the first aerial shoot is usually plumular in origin, shoots may also arise from the haustorial disc region and/or from the endophytic system, particularly when the plumular shoot is damaged or lost (York 1909). Information on seedlings of the traditional santalacean mistletoes is sparse (Kuijt 1990).

The pattern of seedling establishment in the highly specialized genus *Arceuthobium* is strikingly different than that described for *Viscum* and *Phoradendron.* In *Arceuthobium* the cotyledons are only rudimentary, and the shoot apex is poorly developed (Cohen 1963). At germination epicotylar growth is suppressed in favor of endophytic establishment (Kuijt 1969). All aerial shoots are rootborne, arising from the endophytic system two or more years after the initial infection (Hawksworth and Wiens 1996). *Phoradendron californicum* Nutt. is reported to have a pattern of establishment similar to that of *Arceuthobium* in that, like *Arceuthobium,* aerial shoots are said to arise exclusively from the endophytic system (Kuijt 1989). In *Viscum minimum* the embryonic shoot apex aborts, and the initial seedling shoots arise from the endophytic system or shoot buds that form on the holdfast or directly below it (Kuijt 1986). The shoot apex of *P. macrophyllum,* a large-leaved species, appears to be more highly developed than that of *Arceuthobium* (compare Cohen 1963, fig. 3, with Calvin 1966, fig. 9). Major changes from the usual

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sequence of seedling growth, such as reduction or suppression of embryonal apical differentiation, seem to be an evolutionary trend in parasitic flowering plants (Teryokhin and Nikiticheva 1982).

For mistletoes in general an insufficient data base exists on seedling structure (Kuijt 1982). This lack of basic information can lead to misinterpretation of life cycle sequences important to physiological, developmental, and taxonomic determinations. During another study (Calvin et al. 1993) we noted a number of unusual seedling features in *P. juniperinum*. This observation, coupled with Kuijt's (1982) comments on the paucity of information on mistletoe seedlings in general, prompted this study. Three additional species of *Phoradendron* were included to provide a comparative dimension to the study and to broaden its focus. Our field and laboratory studies indicate that a greater variation in seedling morphology exists within the genus than has been reported.

Materials and Methods

The four species of *Phoradendron* chosen for this study were: *P. californicum* (desert mistletoe), *P. densum* Trel. (dense mistletoe), *P. juniperinum* A. Gray (juniper mistletoe), and *P. villosum* (oak mistletoe). For *P. juniperinum,* the primary focus of the study, several hundred seedlings were examined. Fewer specimens (100–200) were analyzed for each of the other species studied. More than one population was utilized for 3 of the species, as indicated below. The 4 species studied occur at the northern limit of the *Phoradendron* range. Two of the species, *P. californicum* and *P. juniperinum,* are squamate; that is, their leaf blades are scale-like. *Phoradendron densum* has small leaves, and *P. villosum* has leaves of medium size (as compared to *P. macrophyllum*).

Specimens of the four *Phoradendron* species were collected at intervals during the years 1984–1987. The materials of *P. californicum* were collected in proximity to Mesquite, NV, Oatman, AZ, and on the Cabezon Indian Reservation near Indio, CA. The host trees were primarily *Prosopis,* but specimens were also collected from *Acacia, Cercidium* and *Larrea. Phoradendron densum* was collected 6.5 miles downstream from the J. C. Boyle Powerhouse in Klamath Canyon, OR, and in the vicinity of Weed and Henley, CA. The host tree was *Juniperus. Phoradendron juniperinum* was collected in and near Bend, OR, also growing on *Juniperus. Phoradendron villosum* was collected in two widely separated localities: near Corvallis, OR, and 30 miles east of Red Bluff, CA, along State Highway 36. *Herbarium* specimens of the four species studied are deposited in the Portland State University Herbarium (HPSU). For all species, collected specimens were brought to the laboratory and examined while fresh, using a Zeiss dissecting microscope. Some specimens were preserved in al-

cohol for further study. Description of gross shoot morphology centered on the nature of the cotyledons (number, size, fused or free, persistence, visibility), the origin of aerial shoots (plumular, haustorial disc region, endophytic system), the fate of aerial shoots, internode extension, and length of the hypocotyl.

In this study three categories of aerial shoots are recognized: 1) *Plumular shoots,* arising from the shoot pole of the embryo; 2) *Nonplumular seedling shoots,* arising from the haustorial disc or cushion region; and, 3) *Root-borne shoots,* arising from the endophytic system. Nonplumular seedling shoots probably represent a type of root-borne shoot; but they are segregated here since a major focus of this report is on the contrasting origins of aerial shoots in the species studied. Further, since the morphological nature of the holdfast and cushion regions remains problematic, a distinction is justified.

Results

In the Bend, OR, area the fruits of *Phoradendron juniperinum* reach maturity in early winter. Several bird species feed on these fruits and void seed on nearby host branches (Fig. 1). Shortly thereafter germination begins. In *P. juniperinum* (Figs. 1–12) and the other *Phoradendron* spp. examined the radicle is the first structure to emerge from the seed (Fig. 1). The specimen shown was collected in mid-May and reflects the slow but continuous growth of the green hypocotyl-root axis. Eventually the root tip reaches a penetration site, which is typically, but not always, beneath a scale leaf, and form a holdfast (Fig. 2). Throughout this stage the cotyledon tips remain more or less embedded within the endosperm, which is in turn covered by the sclerophyllous "seed" coat (Fig. 2). As growth continues, the seedling becomes erect, shedding the remnants of the endosperm, and the plumular shoot develops (Fig. 3).

At this stage of seedling growth striking differences between seedlings become evident. In many seedlings an expanded region of tissue, here designated the haustorial cushion, develops beneath the holdfast raising it above the host surface (Fig. 4). Of 254 seedlings studied for this feature 52% developed a cushion. Typically, 2–4 vegetative buds arise on the cushion (Fig. 4), but as many as 11 were observed. These buds may remain dormant for a time (Fig. 4) or initiate shoot growth almost as soon as they appear (Fig. 5). Seedlings that failed to form a cushion did not develop nonplumular seedling shoots at the initial infection site. Root-borne shoots may develop later, however, directly from the endophytic system. The development of shoots from the endophytic system is a common phenomenon in some viscacean genera and has been observed by several workers (Bray 1910; Cannon 1901; Kuijt 1969; York 1909).

In approximately 20% of specimens studied,
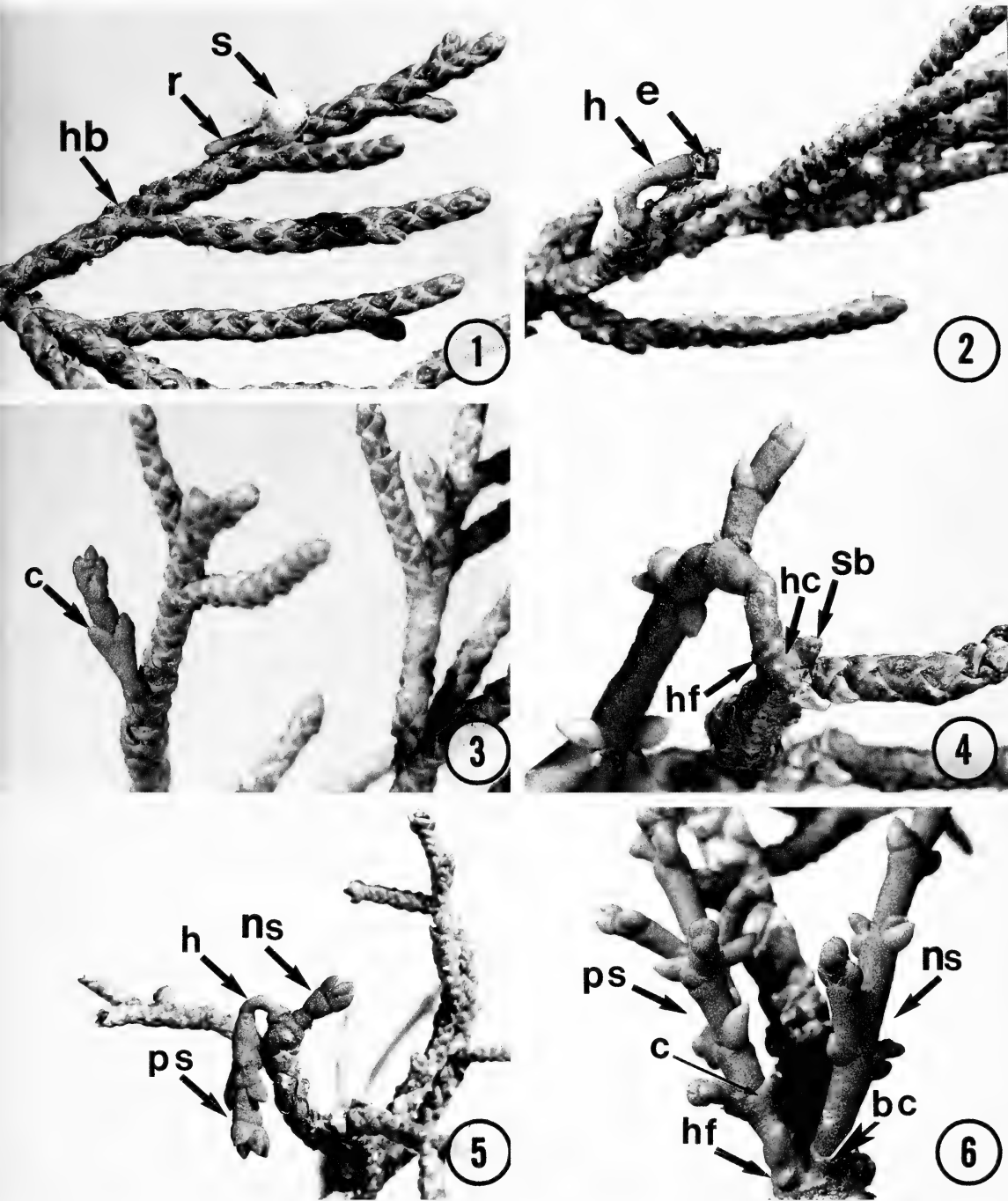
FIGS. 1–6.   *P. juniperinum.* Fig. 1, germinating seed, s, with elongate hypocotyl-root axis, r. Fig. 2, seedling with elongate hypocotyl, h, and holdfast label? Fig. 3, seedling with cotyledons, c, and plumular shoot. Fig. 4, young plant showing holdfast, hf, haustorial cushion, hc, and vegetative shoot bud, sb. Fig. 5, seedling with curved hypocotyl, prominent holdfast, young plumular shoot, ps, and developing nonplumular shoot, ns. Fig. 6, young plant with well-developed plumular and nonplumular seedling shoots; note basal cup, bc, present at base of nonplumular seedling shoot; endosperm remains, e; host branch, hb. All ×1.

nonplumular seedling shoots originating on the haustorial cushion equaled (Fig. 6) or surpassed plumular shoots in size by the time the latter had five extended internodes. Nonplumular shoots can be identified by a basal, cup-like structure, presumably the lowermost leaf pair. Plumular shoots, in contrast, have a holdfast, a hypocotyl and cotyledons (Fig. 6).

A particularly interesting feature observed in some *P. juniperinum* seedlings is the virtual absence of growth from the plumular apex. This phenomenon was noted in about 10% of the seedlings examined. In this event, the growth of nonplumular shoots displaces the original seedling to a lateral position near the base of the developing nonplumular seedling shoots (Figs. 7–9). The remnants of the initial seedling are persistent and have been seen on infections in which developing shoots had ten or more extended internodes. When first observed these small, undeveloped "basal" seedlings were interpreted to be autoparasites, but as developmental stages were examined the true nature of these seedling structures became evident.

Nonplumular seedling shoots often appear more vigorous than shoots developing from the embryonic shoot apex. This vigor may be related to several factors. Frequently nonplumular shoots have a darker green color than plumular shoots (Fig. 9), possibly reflecting a higher content of chlorophyll. A constriction, not seen in other shoots, is often evident in the hypocotyl region of plumular shoots immediately above the holdfast (Fig. 10). Additionally, extreme curvature of the hypocotyl can occur in this region (Fig. 11). These features may diminish the quality and quantity of the vascular connection between shoot and root. Constriction and/or curvature may also represent a weak point, since seedlings broken off in this region were observed in the field.

Phoradendron juniperinum generally has two cotyledons (Fig. 3) although the number ranges from one to three. Usually the cotyledons are free and spreading; that is, plants display phanerocotyly (Figs. 3, 6). In some cases the cotyledons may be partially or wholly fused along one edge; rarely they are fused to such an extent that the demarcation between the individual cotyledons is difficult to discern (Fig. 12). The cotyledons display a set of morphological characteristics that distinguishes them from subsequent leaves. First, their extreme tips (approximately 1 mm) are seen to be pointed and chlorotic upon removal of the endosperm. Later the points appear brown and withered. These minute tips are nearly always present, and can be seen when cotyledons are examined closely. Second, the cotyledons join smoothly and without interruption with the hypocotyl region (Fig. 3), whereas the subsequent scale leaves often have a definite line of demarcation at their junction with the stem (sl in Fig. 9). Third, the cotyledons are not deciduous, whereas in species with foliage leaves (but not in

P. juniperinum) the latter are deciduous. Although the shape of cotyledons changes as stem diameter increases, they can still be recognized on specimens such as that seen in Figure 12, which has over 20 extended internodes. Using these criteria the presence of cotyledons can be used to distinguish between plumular and nonplumular shoots in the field.

Phoradendron densum (Figs. 13–18) follows closely the sequence of events described for early seedling growth of *P. juniperinum*. Following germination and holdfast formation, the seedling becomes erect (Fig. 13). A haustorial cushion may also form, but not as commonly as in *P. juniperinum*. Of 121 specimens examined, 37% had a haustorial cushion. Generally one or two shoot buds are initiated on the cushion, but 90% of these had not developed into shoots even after seven extended internodes were visible on the plumular shoot. It was noted, however, that all buds produced shoots in the six cases where the original seedling had been damaged by herbivory or mechanical injury. This species frequently produces root-borne shoots directly from the endophytic system, and large clusters of these shoots are found at varying distances from the initial infection site. In none of the plants examined did we observe arrested plumular shoot growth as illustrated in Figures 7–9 for *P. juniperinum*.

The cotyledons of *P. densum*, typically two or three in number, display the distinct morphological features described for *P. juniperinum* (Fig. 14). Fusion of the cotyledons is common, occurring at their tips (Fig. 15), along their margins (Fig. 16), or a combination of these (Fig. 17). In any event, the cotyledons do not appear to enlarge very much and remain smaller, although somewhat more succulent, than subsequent foliage leaves. With continued lateral expansion of the main stem, the cotyledons may assume a position perpendicular to the stem axis, and they persist even after foliage leaves above them are lost (Fig. 18). As in *P. juniperinum*, the presence of cotyledons is a reliable indicator of plumular shoots.

Seedling development in *P. californicum* (Figs. 19–24) differs from that of both *P. densum* and *P. juniperinum*. Upon germination the extending radicle, which is distinctly reddish in color, forms a holdfast from which the endophyte is established (Fig. 19). Seedlings may then become erect with respect to the host branch (Fig. 19) or remain in the same plane as the host branch (Figs. 20–22). At about the same time a thin to somewhat thickened haustorial cushion forms immediately below the holdfast, elevating the holdfast above the branch surface (Figs. 20, 22). From the cushion region an average of seven, but as many as 20, shoot buds are formed (Fig. 23). When a large number of shoot buds are formed, they may be present around the entire periphery of the cushion, eventually forming shoots that radiate outward in
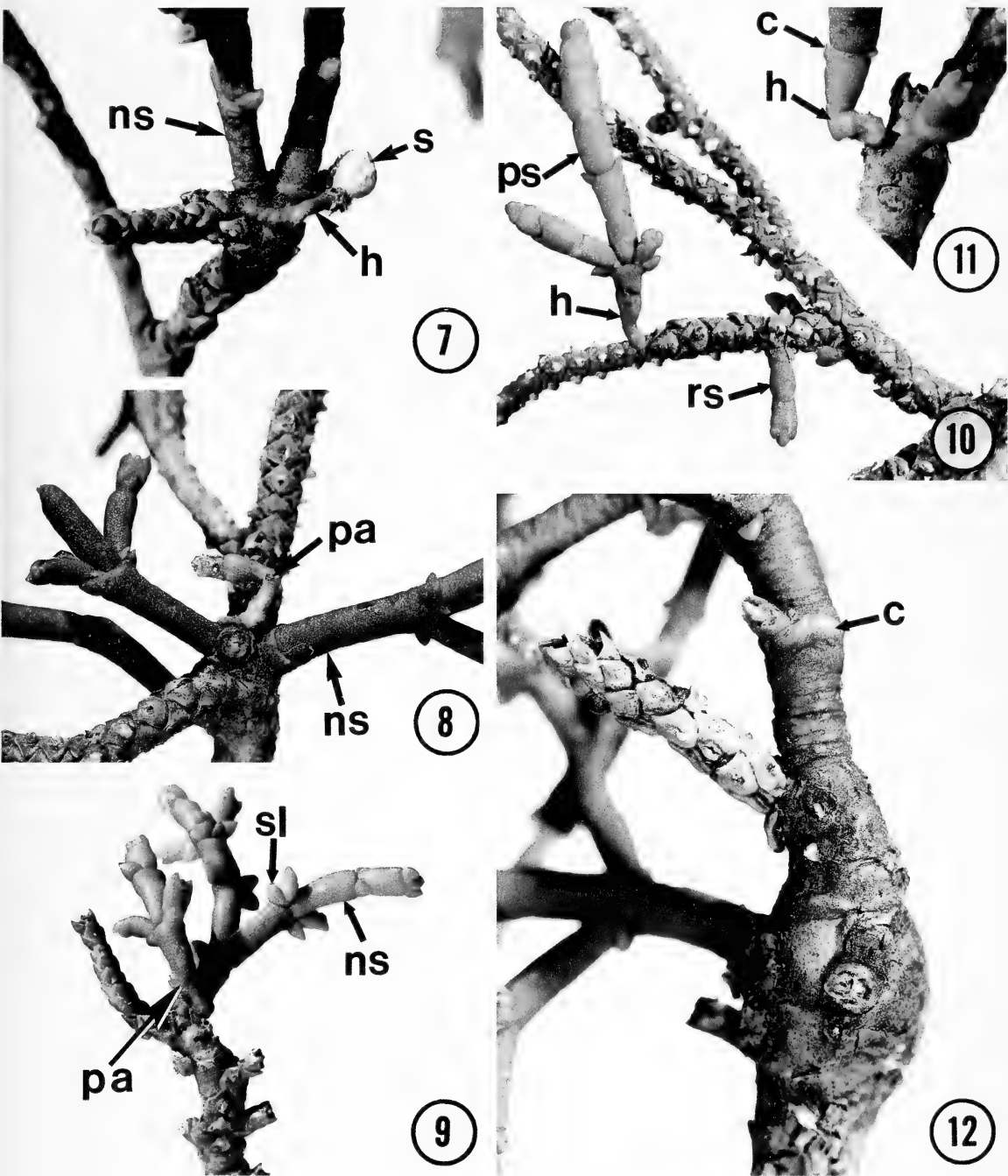
FIGS. 7–12. *P. juniperinum.* Fig. 7, nonplumular seedling shoot, ns, with undeveloped plumular axis at base as evidenced by seed, s, with developed hypocotyl-root axis, h. Fig. 8, plant with 2 nonplumular shoots and basal, undeveloped plumular axis, pa. Fig. 9, young plant with developing nonplumular shoots and basal plumular axis. Fig. 10, seedling with developed plumular shoot, ps; note constricted hypocotyl and adjacent root-borne shoot, rs. Fig. 11, portion of young plant showing minute cotyledons, c, and contorted hypocotyl. Fig. 12, older plant; fused cotyledons still visible; scale leaf sl. All ×1.

all directions from the initial infection site (Fig. 24). Regardless of their number and distribution, the vast majority of vegetative buds develop, resulting in infections having thick clusters of shoots. Shoots may also arise from the endophytic system, particularly when the initial infection site is at a node.

In all but one population of *P. californicum* 100% of plumular shoots failed to develop. However, the original seedling remained, often for
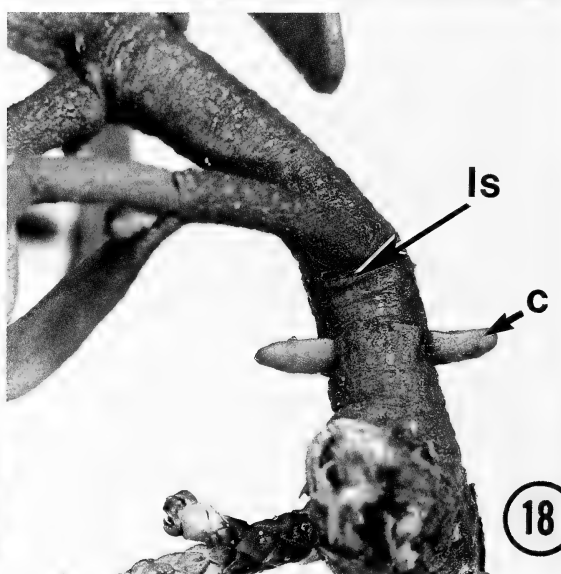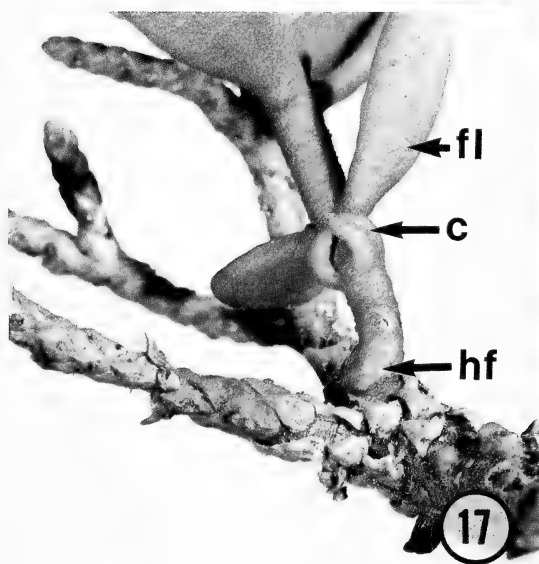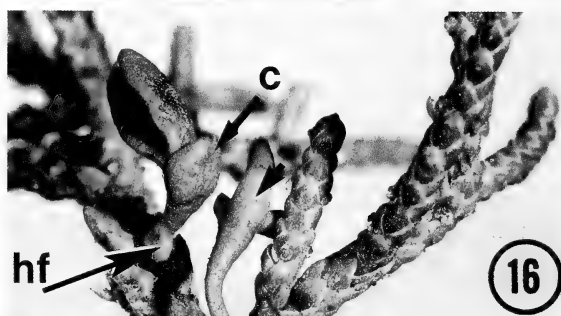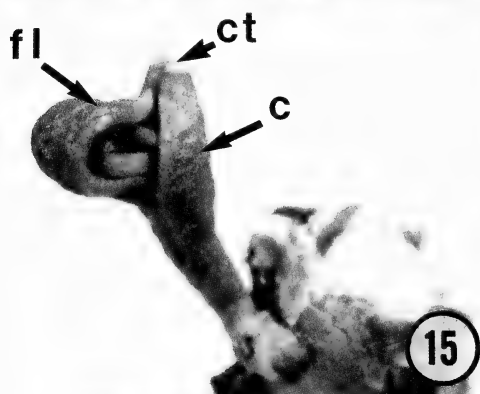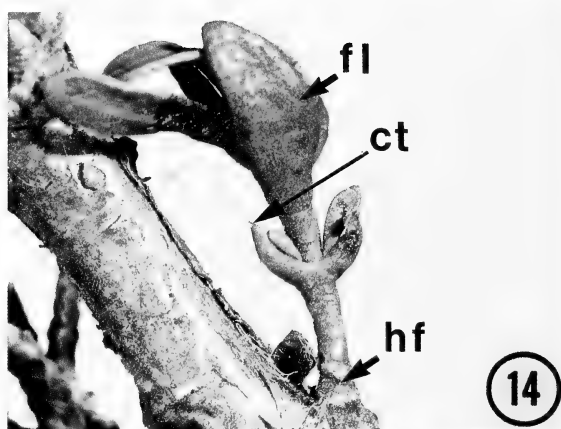
FIGS. 13–18. *P. densum.* Fig. 13, seedling with cotyledons, c; note second seedling at unlabeled arrow. Fig. 14, older seedling with succulent cotyledons and foliage leaves, fl. Fig. 15, seedling with cotyledons united at tip, ct, and emergent foliage leaves. Fig. 16, two seedlings, seedling at left has fused cotyledons and emergent foliage leaves. Fig. 17, seedling with three cotyledons fused both at tips and margins. Fig. 18, older plant with persistent cotyledons, note leaf scar, ls, at adjacent node; holdfast, hf. All ×1.

years, as a usually living hypocotyl-root axis in amongst the developing nonplumular seedling shoots (Fig. 24). In some cases the elongate hypocotyl-root axis becomes erect, and remnants of the endosperm may remain visible, obscuring the cot-

yledons (Fig. 22). Although not always readily visible, the location of the failed plumular shoot clearly identifies the initial site of infection. In the Cabezon Indian Reservation population, in contrast, the plumular shoot had developed in 5 of 17 newly
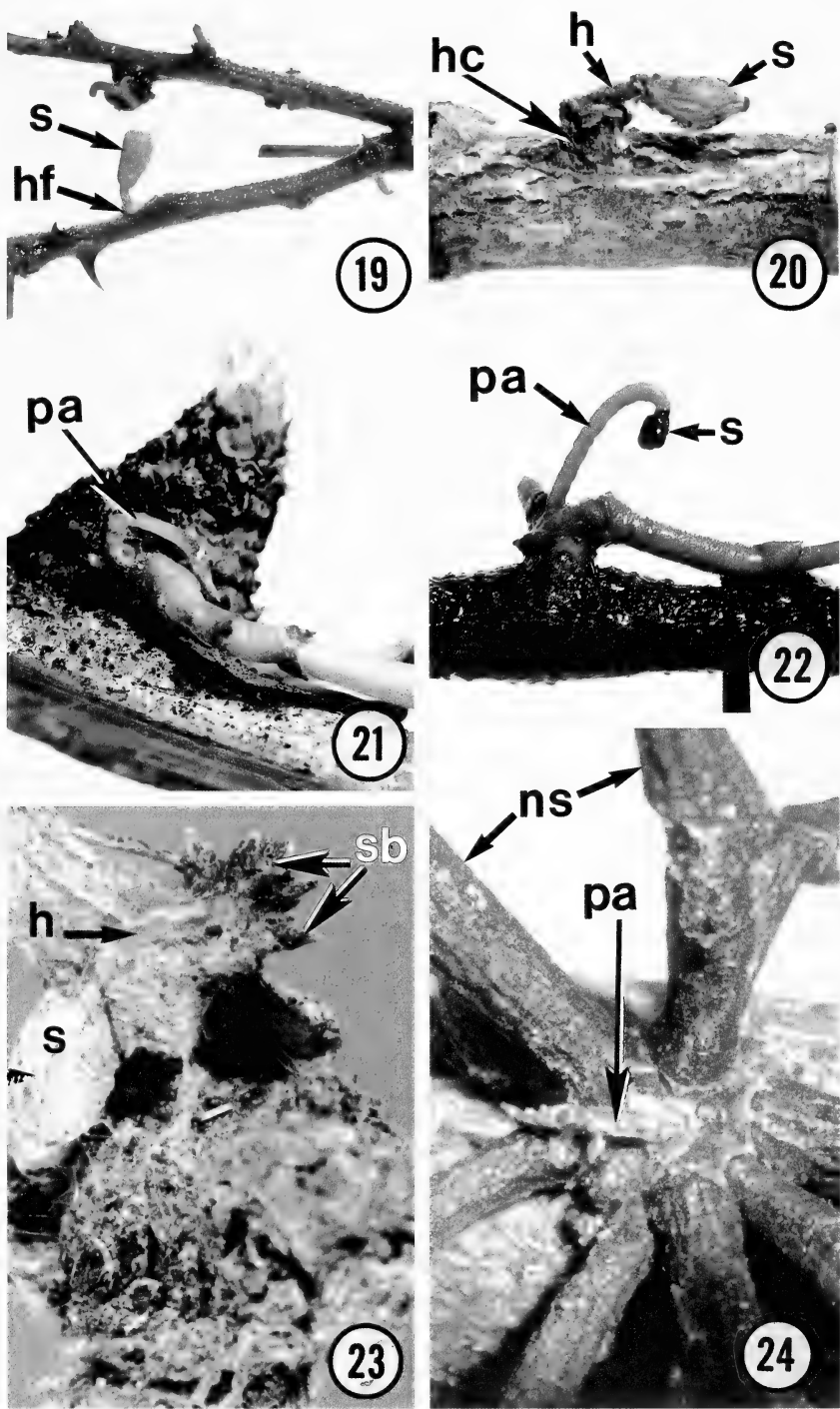
FIGS. 19–24.   *P. californicum.* Fig. 19, germinated seed, s, with holdfast, hf. Fig. 20, germinated seed that has entered host tissue; note elevated haustorial cushion, hc, beneath holdfast. Fig. 21, young plant with undeveloped plumular axis, pa, at base of nonplumular shoot. Fig. 22, young plant with erect, undeveloped plumular axis at base of nonplumular shoot. Fig. 23, germinated seed with elongate hypocotyl, h, and several vegetative shoot buds, sb, radiating outward from the haustorial cushion. Fig. 24, older plant with seven nonplumular shoots, ns; note plumular shoot axis at center of radiating shoots. All ×1.

established seedlings examined. In these seedlings the endosperm mass had been shed and the cotyledons were clearly visible. In size and form, the cotyledons resembled those of *P. juniperinum*. All of the seedlings had two cotyledons, and in none were the cotyledons fused.

Seedling establishment in *P. villosum* resembles closely establishment events described previously for *P. macrophyllum* (Calvin 1966). Dispersed seed lie flat upon the host branch. At germination the elongating hypocotyl-root axis makes contact with the host branch and a holdfast is formed (Fig. 25). Subsequently seedlings become erect (Figs. 26, 27) and the plumular shoot begins its development. In all seedlings and juvenile plants examined two separate cotyledons were evident. As in the other species described herein the cotyledons were small with brownish, pointed tips. Also, the cotyledons were persistent, remaining on the plant long after later-formed leaves had abscissed (Figs. 26, 27). Finally, as in the other species, the internode immediately above the cotyledons frequently showed little or no elongation (Fig. 26). In none of the more than 25 seedlings examined was a haustorial cushion evident, and in none of the specimens were shoot buds present at the infection site. Presumably, root-borne shoots can develop from the endophytic system of *P. villosum*, as occurs in other *Phoradendron* species, but none were observed in the specimens examined. Instead, younger shoots were seen to have two small but persistent cotyledons (Fig. 27).

The seedling establishment events described above for four *Phoradendron* species share features in common with seedling establishment in other viscoid genera, as well as in *Tupeia*, a member of the Loranthaceae. In Figure 28 is shown a seedling of *Viscum rotundifolium* collected in South Africa. Visible are the holdfast, elongate hypocotyl, and two small, persistent cotyledons with pointed ends (shown enlarged in Fig. 29). Note also that the internode directly above the cotyledons did not elongate, as is common in *Phoradendron*. In Figure 30 is shown a seedling of *Notothixos subaureus* collected near Wisemans Ferry, New South Wales, Australia. The seedling has a holdfast, an erect, elongate hypocotyl and two minute cotyledons. Immediately above the cotyledons are two shoots. It appears that both of these shoots arose from axillary buds following injury to the main, plumular shoot. Finally, more than 100 seedlings of *Tupeia antarctica*, growing on tree lucerne on the Banks Peninsula near Christchurch, New Zealand, were examined for seedling characters. Remarkably, more than one third of these seedling showed small, arrested plumular shoots near the base of their developed nonplumular seedling shoots, a situation almost identical to that illustrated for *P. juniperinum* (Figs. 7–9) and *P. californicum* (Figs. 21–24).

DISCUSSION

Dispersed and germinating seed of the *Phoradendron* species studied lie flat on the host branch; that is, their smallest dimension is perpendicular to the branch surface. A similar placement is found in the viscoid genera *Arceuthobium* (Hawksworth and Wiens 1996), *Notothixos* (McLuckie 1923) and *Viscum* (Salle 1983; Kuijt 1986). Dispersed and germinated seed of many loranth genera also lie flat against the host branch (Polhill and Wiens 1998; McLuckie 1923; C. L. Calvin personal observation). This stands in marked contrast to the dispersed and germinating seed of the loranth genera *Alepis* and *Peraxilla* which stand on end (Ladley et al. 1997). In these genera the root tip points away from the host branch, and the elongating hypocotyl-root axis curves 180 degrees to contact the host. This contrasting orientation apparently relates to the distribution of viscin in fruits. In both *Alepis* and *Peraxilla* the viscin is positioned in a ring near one end of the seed (Ladley et al. 1997), whereas in the viscoids studied the viscin is dispersed more evenly around the seed.

The formation of a haustorial cushion is described for three of the species studied. This cushion arises at the base of the holdfast and is the site of origin of nonplumular seedling shoots. In *P. juniperinum*, which has the most pronounced cushion, its development may raise the holdfast well above the surface of the host branch. Kuijt (1986) noted that in *V. minimum* seedlings aerial shoots may also arise from directly beneath the attachment disc, as well as from the margin of the disc. York (1909) found that in *P. macrophyllum* "the aerial shoots which are first formed usually arise from buds, which develop on the attachment disc. . . ." In the present study shoot buds were not seen to arise on the attachment disc (holdfast), but rather on the cushion of tissue formed directly beneath the holdfast. The shoots of *V. minimum* that arise beneath the holdfast (Kuijt 1986) presumably also arise from a cushion-like region.

The first aerial shoots of *Phoradendron* seedlings have generally been regarded as being plumular in origin (Cannon 1901; York 1909; Calvin 1966). In the present study the initial shoots of *P. densum* and *P. villosum* were exclusively plumular in origin, whereas those of *P. californicum* were almost entirely nonplumular. Seedling shoots in *P. juniperinum* were either plumular or, somewhat less commonly, nonplumular in origin. Where plumular shoot growth is arrested shoots arise from shoot buds initiated on the haustorial cushion formed beneath the holdfast. Additionally, root-borne shoots may be formed in proximity to the infection site (see rs in Fig. 11), particularly in *P. californicum*. These contrasting patterns of shoot origin represent a greater diversity than previously recognized. The situation in *P. californicum* approaches that in *Arceuthobium* spp. (Cohen 1963; Hawksworth and
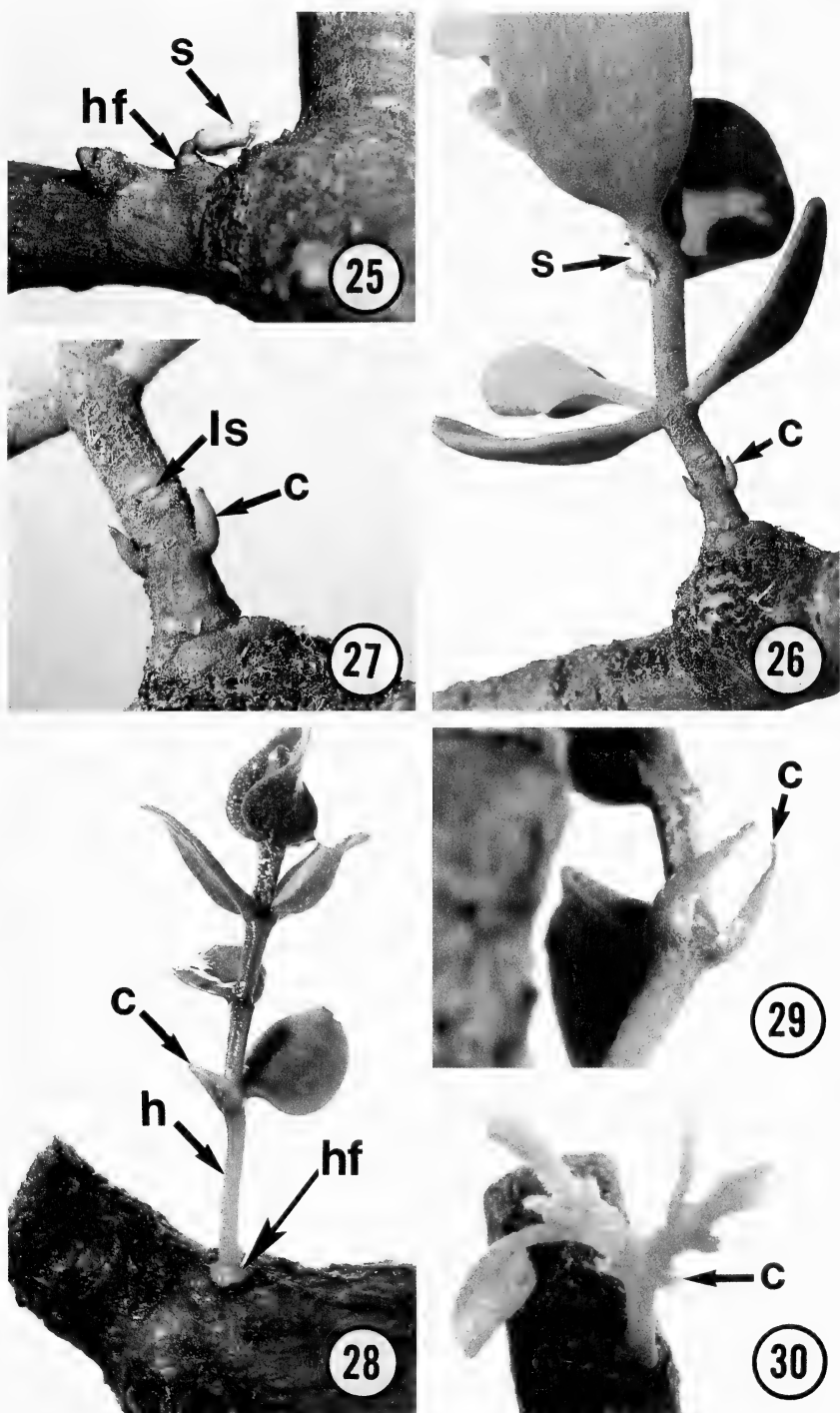
FIGS. 25–30.   *P. villosum* (Figs. 25–27), *V. rotundifolium* (Figs. 28, 29) and *N. subaureus* (Fig. 30). Fig. 25, germinated seed with well developed holdfast, hf. Figs. 26, 27, seedling with two cotyledons; note leaf scar, ls, above and directly opposite cotyledons. Figs. 28, 29, young plant with elongate hypocotyl-root axis, holdfast and free cotyledons (one of the two leaves attached at the node directly above cotyledons was removed to enhance visibility of cotyledons). Fig. 30, seedling with two minute cotyledons and small plumular shoot; cotyledon, c, hypocotyl-root axis, h, seed mass, s. All ×1.

Wiens 1996) and in *Tristerix aphyllus* (Mauseth et al. 1984) where the initial shoot and all succeeding shoots are root-borne. In *P. californicum,* however, the first aerial shoots arise from an aerial portion of the seedling, not from the endophytic system as has been reported (Kuijt 1989). In *Arceuthobium* and *T. aphyllus,* on the other hand, the initial shoots arise from the endophytic system and do not appear for some time after penetration of the host branch; about two years in *Arceuthobium* spp. (Hawksworth and Wiens 1996).

The cotyledons of the *Phoradendron* species studied varied in both number and form. Most seedlings of *P. juniperinum* had two cotyledons, but a few had either one or three. In *P. densum* either two or three cotyledons were present, whereas in *P. villosum* all seedlings had two cotyledons. The few plumular shoots of *P. californicum* observed in the Cabezon population also had two cotyledons. The cotyledons of *P. densum* were the largest and most succulent in appearance, those of *P. juniperinum* and *P. villosum* were intermediate in size and those of *P. californicum* the smallest. Fused cotyledons were common in *P. densum,* but rare or absent in the other *Phoradendron* species. Observations of earlier workers on the fate of cotyledons are in conflict. Bray (1910) states that in *P. macrophyllum* the cotyledons become erect and slowly expand as the first pair of green leaves. York (1909), on the other hand, states that the cotyledons either wither or become slightly enlarged but never form foliage leaves. Our observations are more similar to those of York. Of interest, in all 4 species the cotyledons were persistent, as are the scale leaves of the squamate species. In contrast, the subsequently formed foliage leaves of *P. densum* and *P. villosum* are deciduous. Persistent cotyledons that do not develop into foliage leaves are considered unusual, and Sporne (1974) cites only two examples of this phenomenon, both in the family Gesneriaceae.

Phoradendron densum and *P. villosum* were consistently phanerocotylous. The vast majority of specimens of *P. juniperinum* were also phanerocotylous, but in occasional specimens, such as those shown in Figures 7 and 8, the cotyledons never emerge. In contrast, in only a single population of *P. californicum* were seedlings observed in which the cotyledons were visible and spreading. It is probable that the ancestor of the viscoids was phanerocotylous, as are the majority of modern viscoid species. In agreement with Kuijt (1990) we regard the cryptocotylar condition observed in highly specialized, squamate species of *Phoradendron,* illustrated here by *P. juniperinum* and *P. californicum,* to be advanced. Cryptocotyly is regarded by some as the ancestral germination pattern in angiosperms as a whole (Gifford 1991).

The four *Phoradendron* species examined show a progressive reductional trend in leaf size. Leaves of *P. villosum* are of intermediate size (compared to those of *P. macrophyllum,* for example), those of *P. densum* are small and those of *P. juniperinum* and *P. californicum* are reduced to scales. The four also display reductional trends in seedling development. In this series plumular shoots give way to nonplumular seedling shoots developing on a haustorial cushion, and phanerocotyly is replaced by cryptocotyly. This trend is carried even further in *Arceuthobium* species. In all members of this genus aerial shoots are root-borne, and neither plumular shoots nor nonplumular seedling shoots are ever formed (Hawksworth and Wiens 1996). The significance of these reductional trends is difficult to ascertain. One possible advantage is the formation by seedlings of a larger number of seedling shoots—a sort of tillering—at an early age through the formation of shoot buds either on the attachment disc or on the proliferative tissue formed beneath the attachment disc. Also, as noted earlier, nonplumular seedling shoots frequently appear more vigorous than plumular shoots when both occur together in a seedling. Finally, species capable of forming nonplumular seedling shoots and/or root-borne shoots have much greater vegetative and reproductive versatility than those relying solely on plumular shoots.

Reduction in or suppression of plumular shoot growth is common in the viscoid mistletoes. It is illustrated here for *P. juniperinum* and *P. californicum,* and described elsewhere for *V. minimum* (Kuijt 1986) and *Arceuthobium* (Kuijt 1969; Hawksworth and Wiens 1996). Reduction in or suppression of plumular shoot growth also occurs in some Loranthaceae. In the New World loranth *T. aphyllus,* all seedling aerial shoots are reported to be root-borne (Mauseth et al. 1984), a condition analogous to that in *Arceuthobium* species. The frequent absence of plumular shoot growth is also reported here for the monotypic New Zealand loranth, *Tupeia antarctica.* It is probable that the suppression of plumular shoot growth occurs to a lesser or greater degree in other genera of viscoids and loranths as well. In *Phoradendron* and other viscoids the suppression of plumular shoot growth is positively correlated with the squamate habit. It is interesting that the suppression of plumular shoot growth is common in species that are considered specialized within their respective clades when it represents a basic growth pattern.

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POLYPLOIDY AND SEGREGATION ANALYSES IN *DELPHINIUM GYPSOPHILUM* (RANUNCULACEAE)

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ABSTRACT

Delphinium gypsophilum Ewan consists of both diploid and tetraploid individuals, but the type of polyploidy (allo- vs. autopolyploidy) has not been documented. Cytotyping using flow cytometry indicated that some populations were 2*n,* others were 4*n,* and several had mixed ploidy. Triploid individuals represented approximately 20% of the sampled plants. There appears to be little geographic structuring of cytotypes. Progeny arrays from controlled crosses provided evidence favoring tetrasomic inheritance, and *Delphinium gypsophilum* has allozyme banding patterns that are consistent with autotetraploidy. Genetic data indicate that polyploids may have formed recurrently, but the exact number of origins and specific progenitor-derivative relationships remain uncertain. Conservation efforts should manage the two cytotypes separately, as they represent potentially different evolutionary units.

INTRODUCTION

Polyploidy is an important phenomenon in the evolution of many plant species. Approximately 47–52% of angiosperms and 44–95% of pteridophytes may have polyploid origins (Grant 1981; Vida 1976). Given the pervasiveness of polyploidy, much remains to be learned concerning its evolutionary consequences. Polyploidy has often been considered to be an evolutionary dead end; however, recent research is revealing that polyploidy is a dynamic process and does not necessarily lead the species toward extinction (reviewed in D. Soltis and P. Soltis 1993, 1999; P. Soltis and D. Soltis 2000). Two types of polyploids exist. Allopolyploids combine the genomes of two diploid species via hybridization and subsequent chromosome doubling. Autopolyploids arise intraspecifically from a diploid progenitor. Because of the differences associated with their origin, allopolyploids and autopolyploids have different modes of inheritance and different genetic attributes. Allopolyploids exhibit fixed heterozygosity and disomic-digenic inheritance. Autopolyploids do not exhibit fixed heterozygosity, but have increased levels of heterozygosity due to polysomic inheritance (often detected as unbalanced heterozygotes; reviewed in D. Soltis and P. Soltis 1993). Taxa that exist as both diploid and polyploid individuals offer a natural laboratory in which further studies can be developed to examine the evolutionary consequences of polyploidy (e.g., shifts in mating systems, Cook and Soltis

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1999, 2000). This paper presents data on the nature of polyploidy in *Delphinium gypsophilum* Ewan.

Delphinium gypsophilum gypsum-loving larkspur, grows in open grasslands in the southern San Joaquin Valley of central California. Two subspecies of *D. gypsophilum* have been described based on size, and to a lesser degree, flower color and range (Lewis and Epling 1954; Warnock 1997). *Delphinium gypsophilum* subsp. *gypsophilum* typically has white flowers that are larger than those of *D. gypsophilum* subsp. *parviflorum* Lewis & Epling (Warnock 1997). *Delphinium gypsophilum* subsp. *parviflorum* has flowers that are usually white, but are often lavender or pink, and this subspecies is typically located closer to the Pacific coast (Lewis and Epling 1954). *Delphinium gypsophilum* subsp. *gypsophilum* consists of both diploid (2*n* = 16) and tetraploid (2*n* = 32) individuals (Lewis et al. 1951), and the two cytotypes are morphologically indistinguishable (Lewis and Epling 1959; J. Koontz pers. obs.). The morphological similarity between diploid and tetraploid individuals of *D. gypsophilum* suggests autotetraploidy. *Delphinium gypsophilum* subsp. *parviflorum* is apparently only diploid (Warnock 1995). Previous genetic work on *D. gypsophilum* (Koontz 2000) does not support the recognition of subspecies, therefore, we treat both subspecies together as *D. gypsophilum* in this study.

In their study of chromosome numbers of most Californian larkspurs, Lewis et al. (1951) cytotyped 378 individuals from 35 populations of *D. gypsophilum* (the subspecies were not recognized in their study). Sixteen populations were diploid, and 19 were tetraploid. Neither populations of mixed ploidy nor triploid individuals were documented (Lewis et al. 1951). Their survey of *D. gypsophilum* sampled populations from throughout the range of the species as it occurred in the 1950's; however, since that time, many populations have been lost because

TABLE 1. POPULATIONS OF *D. GYPSOPHILUM* STUDIED, THEIR PLOIDY, METHOD OF DETERMINATION, AND SAMPLE SIZE *(N)*.
[1] Numerical population designations are from Koontz (2000). [2] Full locality data available from first author. [3] Population grown at WSU.

Population[1]	Locality[2]	Ploidy/method/*N*
1	Kern Co., Hwy 58	3*n*-4*n*/flow/6
2	Kern Co., Hwy 58	2*n*-3*n*/flow/6
3	San Luis Obispo Co., Soda Lake	2*n*-3*n*-4*n*/flow/9
5	Kern Co., Elk Hills	4*n*/flow/6
6	Kern Co., Elk Hills	3*n*-4*n*/flow/7
7	Kern Co., Elk Hills	2*n*-4*n*/flow/4
9	Kern Co., Elk Hills	2*n*-3*n*/flow/5
11	San Luis Obispo Co., Hwy 41	3*n*-4*n*/flow/7
12	San Luis Obispo Co., Hwy 41	2*n*-3*n*/flow/4
13	San Luis Obispo Co., Cypress Mtn. Rd.	2*n*/flow/4
14	San Luis Obispo Co., G14	2*n*/flow/3
15	Monterey Co., New Pleyto Rd.	2*n*/flow/4
16	Monterey Co., Vineyard Canyon Rd.	3*n*/flow/1
17[3]	Merced Co., Los Baños Reservoir	4*n*/squash/5
20	Kern Co., A. D. Edmonston Pumping Plant	2*n*/flow/11
HR[3]	Merced Co., Howard's Ranch, Aqueduct mi. 65	4*n*/squash/5
0[3]	Merced Co., O'Neill Forebay	4*n*/squash/5

of extensive development in the Central Valley of California. *Delphinium gypsophilum* continues to co-exist with human development, but the California Native Plant Society (CNPS) has placed this species on its List 4, a "watch list" of species that may become threatened or endangered. We reexamined the distribution of ploidy in *D. gypsophilum* because the range of *D. gypsophilum* has changed since 1951 and because additional populations of *D. gypsophilum* are now known. If the range of *D. gypsophilum* continues to change and the species becomes threatened or endangered, these data on ploidy will be useful in management plans to ensure the protection of both cytotypes. Additionally, determining the type of polyploidy in *D. gypsophilum* is important for understanding the evolutionary history of this species. The differences between the genetic attributes of allopolyploids and autopolyploids could affect how the cytotypes are treated taxonomically and ultimately managed in conservation efforts.

This study was designed to determine (1) the number, distribution, and similarity of diploid and tetraploid populations, and (2) the mode of inheritance, and therefore the type of polyploid, in the tetraploid cytotype. Flow cytometry and mitotic root-tip squashes were used to determine ploidy of the samples, and their ploidal distributions were plotted along with data from Lewis et al. (1951). To determine the type of polyploid, controlled crosses were performed to generate progeny arrays to test for inheritance patterns of allozyme markers.

MATERIALS AND METHODS

Number, distribution, and similarity of diploid and tetraploid populations. Fifteen populations of *D. gypsophilum* were sampled (Table 1). Leaf material from these populations was sampled in April and

early May, 1999. Two or three leaves were removed from up to 15 individuals per population. These leaves were wrapped in dry paper towels, placed in labeled plastic sandwich bags and shipped on ice overnight to the University of Arizona (UAZ) for flow cytometry analyses following Galbraith et al. (1997). Briefly, protocols for an arc lamp-based flow cytometer (Partec CCAII, Partec GMbH, Munster, Germany) were used with the Galbraith Homogenization Buffer I and DAPI fluorescent stain. Fluorescent microbeads (Alignflow, Molecular Probes, Inc., Eugene, OR) were used to align the instrument, and then samples of *Nicotiana tabacum cv. Xanthi* were run to set up the instrument. Leaf material from known 4*n* *D. gypsophilum* individuals grown at Washington State University (WSU) were sent to UAZ to use as *Delphinium* standards. The samples of known ploidy (either the *Nicotiana* or 4*n* *Delphinium*) were also run at the beginning of each day and rerun at intervals during the day to ensure that the alignment had not drifted. Each sample was run for 10,000–30,000 events. Flow cytometry is an indirect measure of ploidy and is an effective and efficient technique for estimating the ploidy of natural populations (e.g., Burton and Husband 1999; Greilhuber and Obermayer 1999; Husband and Schemske 1998; Keeler 1992; Thompson et al. 1997). Samples from three additional populations of *D. gypsophilum* were maintained in greenhouse culture at WSU. These populations were started in September, 1996, from seed collected in April and May, 1996, from natural populations (Table 1). Mitotic root-tip squashes following Soltis (1980) were performed to determine the ploidy of these populations. Root tips were harvested from five actively growing plants per population. Voucher specimens from each population were collected and are deposited in the Marion
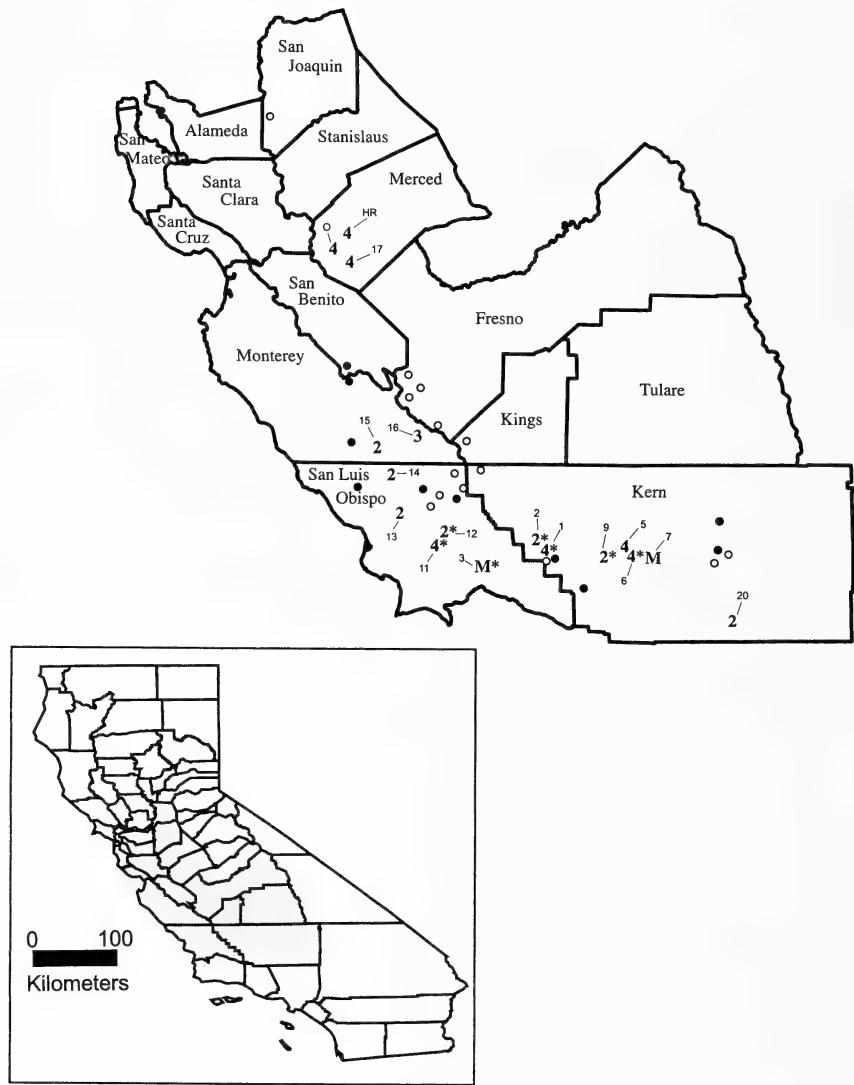
FIG. 1. General location of *D. gypsophilum* populations and their ploidy. Inset: Map of California with counties shaded. Populations from Table 1 are indicated by a connecting line to the ploidy of the samples: 2 = diploid population; 2* = 2n and 3n individuals present; 3 = triploid population (but based on only 1 sample); 4 = tetraploid population; 4* = 4n and 3n individuals present; M = 2n and 4n individuals present; M* = 2n, 3n, and 4n individuals present; open circles = 4n populations surveyed by Lewis et al. (1951); closed circles = 2n populations surveyed by Lewis et al. (1951).

Ownbey Herbarium (WS). Ploidal levels of sampled populations are listed in Table 1. Figure 1 shows the relative locations of the populations studied.

We investigated the similarities among extant populations of *D. gypsophilum* using 12 allozyme loci reported in a previous study (Koontz 2000). These data were originally used to test the hypothesis of hybrid origin of *D. gypsophilum* (Lewis and Epling 1959). The analyses of allozyme data reported here are original. We computed genetic identities (Nei 1972) that were then subjected to clustering analysis (UPGMA) using BIOSYS-1 (Swof-

ford and Selander 1989) to explore which populations were more similar to one another, to determine if the number of origins of tetraploid *D. gypsophilum* could be inferred, and if more than one diploid population was involved.

Mode of inheritance in the tetraploid cytotype. We tested inheritance patterns by crossing cultivated plants of known allozyme genotype to generate progeny arrays. The crossing design, number of progeny scored, and allozyme genotypes are listed in Table 2. Controlled crosses were performed in the Steffen Center Greenhouses, WSU, during Feb-

TABLE 2.   CROSSING DESIGN FOR *D. GYPSOPHILUM* TO TEST FOR TETRASOMIC INHERITANCE.

Cross	Source population (individual)	Locus	Cross genotype	No. of progeny scored
1a	O'Neill (30) × O'Neill (42)	*Pgm*	*bbbc* × *bbbc*	71
1b		*Aat-1*	*bbbc* × *bbbb*	84
2	O'Neill (35) × O'Neill (37)	*Lap*	*aacc* × *aaaa*	81
3a	Los Baños (26) × O'Neill (30)	*Lap*	*aacc* × *aaaa*	88
3b		*Aat-1*	*bbbb* × *bbbc*	82
4a	Los Baños (9) × Los Baños (11)	*Pgm*	*bbbd* × *bbbb*	51
4b		*Lap*	*aacc* × *aaaa*	57

ruary–March, 1997. Seven plants were selected based on their previously determined allozyme genotype (Table 2). For each cross, 10 flowers per plant were cross-pollinated in the following manner. Flowers were emasculated just prior to opening. The removal of the anthers triggered the stigmatic surface to become receptive two days later, when pollen was transferred to the stigma. Each cross was performed reciprocally. Fruits were harvested at maturity, just before or at dehiscence (approximately 3–4 weeks after pollination). The fruits and seeds were stored in paper coin envelopes at room temperature. Previous work on this species indicated that the seeds remain viable for many years, but only germinate when planted in the early fall (JAK pers. obs.). The seeds were planted in plastic flats using regular potting soil in September, 1999. As soon as the seedlings had produced their first true leaves, they were harvested for allozyme electrophoresis.

Allozyme procedures followed Soltis et al. (1983), with the exceptions listed below. Up to 96 individuals per cross were harvested. The fresh leaves were ground, and the wicks were frozen as described by Cook and Soltis (1999). All starch gels were 12.5% (w/v). Buffer system 6 was used to resolve aspartate aminotransferase (AAT). System 8, as modified by Haufler (1985), was used to resolve leucine aminopeptidase (LAP) (stain recipe in McDonald 1985). The morpholine system (Odrzykoski and Gottlieb 1984) at pH 6.1 was used to resolve phosphoglucomutase (PGM). Isozymes were numbered sequentially starting with the most anodal as *1*. Alleles were designated alphabetically, the most anodal as *a*.

A χ^2 test of significance was used to determine if the frequency of progeny genotypes deviated from expected ratios of disomic-digenic and tetrasomic inheritance.

RESULTS AND DISCUSSION

Geographic distribution of cytotypes. Although 15 individuals were sampled from each population for flow cytometry, the leaf material for some individuals was unusable when the flow cytometry was conducted (Table 1). Low sample sizes for some populations may therefore fail to reflect the proportions of diploid and tetraploid individuals accurately.

Populations were either $2n$, $4n$, or of mixed ploidy (Table 1), and 18 individuals (approximately 20% of the 92 samples cytotyped) were interpreted from the flow cytometric data as $3n$ (in population #16, the only individual was $3n$). In an abstract, Lewis (1946) reported the occurrence of natural triploid hybrid individuals in areas of contact between diploid and tetraploid cytotypes of *D. gypsophilum*. However, Lewis et al. (1951) sampled between 1 and 48 individuals per population (mean = 10, standard deviation = 12) from 35 populations, but they did not detect any $3n$ individuals or populations of mixed ploidy in that study. The high frequency of triploids we detected by flow cytometry is surprising given that Lewis et al. (1951) detected no triploid individuals with broader sampling. Other studies have detected triploids, but at lower frequencies [e.g., 1.4% in *Heuchera grossulariifolia* Rydb. (Thompson et al. 1997), 9% in *Chamerion angustifolium* (L.) Holub (Husband and Schemske 1998), and 11% in *Galax urceolata* (Poin) Brumintt (Burton and Husband 1999)]. The coefficients of variation for the *Delphinium* samples measured on the flow cytometer ranged from 3.3 to 41, the average being 10.5 ± 0.74 (SEM). The CVs were high because some of the field-collected samples had started to degrade and were therefore less than optimal for flow cytometry.

In assigning ploidy to the samples, the values set for each ploidy class were arbitrary, but were calibrated on the values obtained from the known $4n$ samples. To determine the effect of changing the boundaries of the $2n$ and $4n$ ploidy classes on the number of $3n$ samples inferred, we broadened the range of $2n$ and $4n$ classes by 10%, but this change only reduced the triploid frequency to 15%. Given the discrepancy in the number of $3n$ individuals observed here and by Lewis et al. (1951), future work is needed using both flow cytometry and mitotic or meiotic squashes.

Geographic structure among related diploids and polyploids has been commonly reported (e.g., Husband and Schemske 1998; Ness et al. 1989; Soltis 1984). Polyploids often have broader ecological amplitudes, in part due to their increased levels of

genetic variation, that allow them to occupy habitats that are inhospitable to their diploid progenitors. This structuring leads to the successful establishment of the polyploid race by ensuring individuals of the same ploidy do not co-occur. The distributions of the cytotypes reported here show little geographic structure. However, the tetraploid populations are clustered in Merced County and in central San Luis Obispo County to western Kern County (Fig. 1). Diploid populations (containing no $3n$ or $4n$ individuals) appear on both sides of the Monterey-San Luis Obispo County line. Many of the populations analyzed by Lewis et al. (1951) no longer exist, though attempts were made to locate them for use in this study. A tetraploid population from San Joaquin County was Lewis et al.'s (1951) northernmost sample, well separated from the other populations of *D. gypsophilum* they surveyed (Fig. 1). Despite several attempts to locate this population, it appears to have been destroyed; nevertheless, the historical presence of this population makes the tetraploid populations discovered in Merced County less isolated. The data from Lewis et al. (1951) indicate that the tetraploids generally clustered around southwestern Fresno County into Kings County, San Luis Obispo County, and in both western and central Kern County.

Other species that exist as both diploid and polyploid populations often display broad geographic structuring of ploidy, but these species all have a much larger geographic range than *D. gypsophilum*. For example, the tetraploid cytotypes of *Heuchera micrantha* Dougl. ex Lindl. occur in the central part of the range, with diploid populations occurring to the north and south (Ness et al. 1989). A distinct north-south distribution is found in *Tolmiea menziesii* (Pursh) Torn & Groy, in which the tetraploid cytotype occurs from southeastern Alaska to central Oregon and the diploid cytotype occurs from central Oregon into northern California (Soltis 1984). Diploid and tetraploid cytotypes of *Chamerion angustifolium* are also distributed latitudinally, with the diploids occurring at higher latitudes (Husband and Schemske 1998). The geographic structure of cytotypes of *Galax urceolata* is less defined because the diploid and polyploid cytotypes overlap; in general, the frequency of diploids decreases north to south, while tetraploids increase (Burton and Husband 1998). The diploid cytotype of *Heuchera grossulariifolia* occurs throughout river systems in Idaho and western Montana, but the tetraploids are more limited in distribution across north-central Idaho into western Montana (Segraves et al. 1999; Wolf et al. 1990).

Multiple origins of polyploid species and cytotypes have been detected in almost all cases that have been investigated (reviewed in Soltis et al. 1992; D. Soltis and P. Soltis 1993, 1999; P. Soltis and D. Soltis 2000). Some of the tetraploid populations in this study cluster geographically with one or more diploid populations (Fig. 1, pops. 1 and 2;

5, 6, and 9; 11 and 12). Additionally, some populations are of mixed ploidy, containing both diploids and tetraploids, as well as some triploids (Fig. 1). These distributions suggest the possibility of multiple origins of the tetraploid cytotype from different diploid progenitor populations.

In previous work, allozyme analyses of multiple populations of *D. gypsophilum* (Koontz 2000; raw data available from first author by request) indicate few differences among tetraploid populations, and DNA sequence divergence in the nuclear ribosomal internal transcribed spacer (ITS) regions between the two diploids and one tetraploid sampled is low (~0.17%) (Koontz 2000). Comparisons of the alleles reported in Koontz (2000) found that neighboring diploid and tetraploid populations e.g., pops. 1 and 2; 5, 6, 7, 8, and 9; and 11 and 12. show similar allele frequencies at most loci. The genetic identities (Nei 1972) among the populations sampled are high (~88–99%); however, a UPGMA clustering diagram reveals two groups (Fig. 2), one composed mainly of the populations found in eastern San Luis Obispo County, eastern Monterey County, and easternmost Kern County, and the other composed of those populations in western Kern County, northwestern San Luis Obispo County, southwestern Monterey County, and Merced County. Tetraploids and diploids occur in both clusters, and those that occur together geographically [i.e., pops. 1 ($3n/4n$) and 2 ($2n/3n$), 6 ($3n/4n$) and 9 ($2n/3n$), 11 ($3n/4n$) and 12 ($2n/3n$)] generally occur in the same group in the UPGMA phenogram (Fig. 2), consistent with recurrent formation of tetraploid populations from neighboring diploid populations. Other populations from the same geographic area occur in separate groups. Population 7 ($2n/4n$) from the Elk Hills area of Kern County occurs in a cluster separate from other populations from this area [pops. 5 ($4n$), 6 ($3n/4n$), and 9 ($2n/3n$), where pop. 5 is more similar to pops. 1 and 2 than to pops. 6 and 9]. Both populations 3 and 7 contain mixed cytotypes, suggesting that the $4n$ cytotype could have arisen within each of these two populations. These data do not provide conclusive evidence of specific progenitor-derivative relationships; however, they are consistent with more than a single origin of the tetraploid cytotype. To test the hypothesis of multiple origins of polyploidy thoroughly, additional populations will need to be sampled both cytologically and genetically.

Segregation analyses. Although no differences in seed set were observed between reciprocal crosses, the seed produced from parent individuals 9 and 11 (crosses 4a and 4b) had low germination, and only 68 progeny were harvested. The numbers of progeny scored for each cross are lower than the total harvested (Table 2) because some individuals did not express well and could not be scored with confidence.

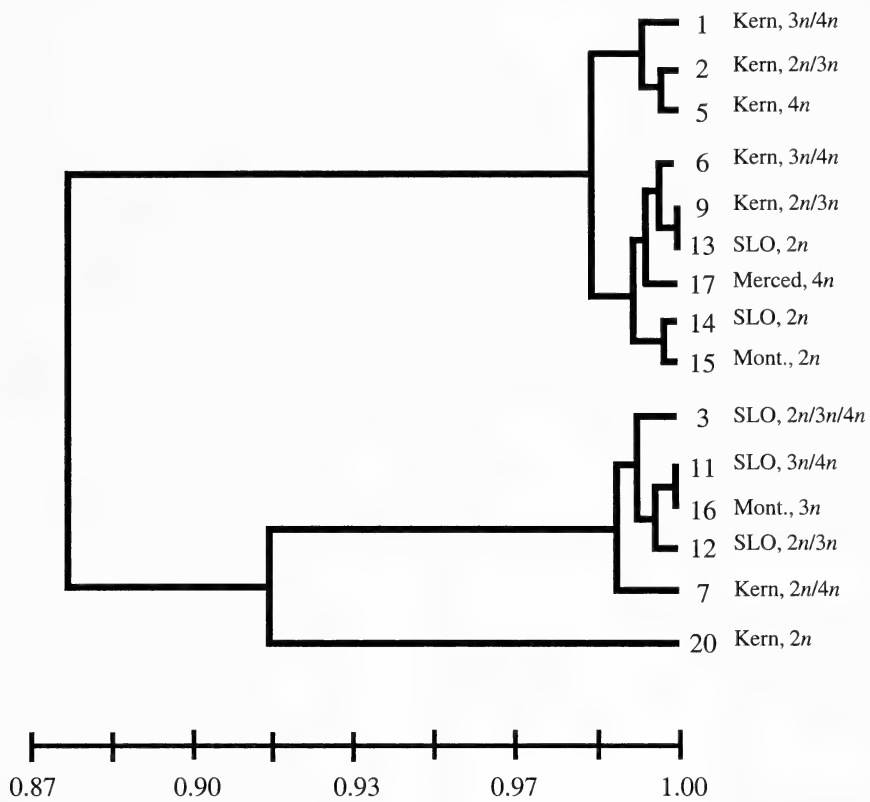Allopolyploids are characterized by fixed hetero-

FIG. 2.   UPGMA phenogram of genetic identity (Nei 1972) for the populations of *D. gypsophilum,* their county, and ploidy. SLO = San Luis Obispo County; Mont. = Monterey County.

zygosity at allozyme loci (e.g., Roose and Gottlieb 1976). Fixed heterozygosity was not observed at any allozyme loci during this or previous work on *D. gypsophilum* (Koontz 2000). At several loci (e.g., *Pgi, Aat, Pgm, Lap*) the tetraploids exhibited unbalanced heterozygotes, indicating dosage effects that may result from either tetrasomic segregation or disomic-digenic segregation with shared alleles at the two loci. Genotypes from progeny arrays were compared with expectations for both tetrasomic and disomic-digenic segregation.

Crosses 1a–b, 3b, and 4a (Table 2) yielded progeny arrays that were consistent with both disomic-

digenic and tetrasomic inheritance models; therefore, χ^2 scores could not distinguish between the two models. For crosses 2, 3a, and 4b (Table 3), progeny were obtained that could only be expected under the tetrasomic model; however, ratios of the observed progeny did not fit the expected tetrasomic ratios (Table 3). Cross 2 had one progeny with an unexpected genotype of *cccc*. These crosses also had a higher proportion of *aaaa* (2), *aacc* (3a), or both *aacc* and *aaaa* (4b) genotypes than expected, and crosses 2 and 4b also had fewer *aaac* progeny than expected.

The progeny arrays from the crossing experi-

TABLE 3.   EXAMPLES OF THE EXPECTED AND OBSERVED PROGENY FREQUENCIES UNDER DISOMIC-DIGENIC AND TETRASOMIC MODELS OF INHERITANCE FOR CROSSES 2, 3A, AND 4B. All are *Lap aacc* × *aaaa. aa,ac* = genotype *aa* at one disomic locus and *ac* at the second disomic locus. NA = genotypes present that are not possible under the given model, making a significance test not appropriate. * The *cccc* genotype was not included in the χ^2 computation, but it would actually make the value "NA" for the tetrasomic model.

Progeny genotype	*aa,cc* × *aa,aa*	*ac,ac* × *aa,aa*	Tetrasomic	2 Observed	3a Observed	4b Observed
aaaa	0.5	0	0.167	0.516	0.159	0.474
aaac	0	1	0.666	0.234	0.5	0.193
aacc	0.5	0	0.167	0.247	0.341	0.333
cccc	0	0	0	0.012	0	0
χ^2	NA	NA	see column under each cross	82.54* $P < 0.0005$	19.718 $P < 0.0005$	41.974 $P < 0.0005$

ments do not offer a clear answer for the mode of inheritance in the tetraploid cytotype. In some cases, the crosses could not distinguish between tetrasomic and disomic-digenic inheritance; these progeny arrays are therefore consistent with both models. In other crosses, the disomic-digenic model could be ruled out because multiple genotypes were recovered that were impossible under the disomic-digenic model without invoking a high frequency of chromatid segregation. However, these same crosses did not statistically fit the tetrasomic model, and one genotype that was not expected under either model appeared in the progeny of one cross. The occurrence of a novel genotype in low frequency in the progeny of a known cross may reasonably be attributed to chromatid segregation (reviewed in Wolf et al. 1989). Additionally, gametic selection has been implicated where progeny arrays derived from the same parents alternately fit perfectly or deviate significantly from expectations when produced and grown in different environments (e.g., Henningsen et al. 1993). Future work should address the possible role of gametic selection.

Conclusions

Using flow cytometry and root-tip preparations, we mapped the cytotypes of *D. gypsophilum* from throughout its current known range. Unlike the previous study (Lewis et al. 1951), we detected mixed ploidy within some populations, as well as triploid individuals. The evidence from allozyme data and the segregation analyses presented here point to tetraploid *D. gypsophilum* as an autotetraploid. Although diploid and tetraploid populations cluster together both geographically and genetically, suggesting recurrent formation of the tetraploid cytotype, the genetic data do not provide conclusive evidence of specific progenitor-derivative relationships among populations.

Conservation implications. The data presented here and elsewhere (Koontz 2000) do not support the subdivision of *D. gypsophilum* into two subspecies. Populations 13, 14, and 15 (all 2n) are from localities that Warnock (pers. comm.) has identified as subsp. *parviflorum*. Population 13 is more similar genetically to populations of subsp. *gypsophilum* (Fig. 2, populations 9, 6, and 17;) than to populations 14 and 15. Furthermore, ploidy does not distinguish the two subspecies. Although all of the tetraploids detected occur in *D. gypsophilum* subsp. *gypsophilum* (Lewis and Epling 1954; this study), five 2n populations are also recognized as subsp. *gypsophilum*.

The combination of genetic and ploidy data suggest that two subspecies should no longer be recognized, even though the subspecies may be distinguished to some degree by range and flower color (but not size). Both subspecies are currently placed on the CNPS List 4. Because the range of *D. gyp-*

sophilum sensu lato continues to be affected by human development, *D. gypsophilum* should remain a List 4 species. Both cytotypes and all morphological variants should be included in any future conservation efforts for this species; the cytotypes should be managed separately, as they represent potentially different evolutionary units.

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SPRING-FED PLANT COMMUNITIES OF CALIFORNIA'S EAST BAY HILLS OAK WOODLANDS

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Abstract

Sixty-eight spring ecosystems containing 207 plant species were sampled in 1991 and 1992 on the East Bay Hills of Alameda and Contra Costa Counties, California. Using TWINSPAN, we identified and described four plant community types: 1) Ryegrass-Herbaceous, 2) Rush-Herbaceous, 3) Willow-Poison oak, and 4) California bay-Poison oak. Spring types were related to environmental gradients and a binary disturbance variable (livestock grazing presence/absence) using canonical correspondence analysis (CCA). Extraction of 2 CCA axes proved useful in relating spring types to productivity (using litter as proxy) and elevation gradients. A third CCA axis indicated that the presence or absence of grazing was somewhat helpful in discriminating among plant community types although gradients found with detrended correspondence analysis (DCA), which uses only the species matrix, were much stronger than could be generated by combining measured environmental and management factors (i.e., CCA). While community type, which was defined by taxonomic abundance, was apparently independent of grazing presence/absence, the grazing axis (CCA_3) was effective in dispersing willow size classes such that overstory willows scored higher on the ungrazed end and shrub willows scored higher on the grazed end of CCA_3. We conclude that grazing can affect vegetation structure of some spring-fed plant communities, but that composition is controlled by site variables.

Classification of California vegetation has a long and varied history. General descriptions of major vegetation types can be found in Jepson (1975), Munz and Keck (1973), as well as Ornduff (1974). More recently, *The Jepson Manual* (Hickman 1993) described major climatic and geographic zones in which plants can be found in California. Sawyer and Keeler-Wolf (1995) described California plant communities based on quantitative analysis of field plot data, or relied heavily on Holland's (1986) qualitative descriptions of communities if plot data were unavailable.

Many vegetation classification systems have been developed for specific purposes. For example, oak woodlands were described to subseries to provide baseline, quantitatively-based descriptive information for the Integrated Hardwood Range Management Program (Allen et al. 1989). Ferren et al. (1994) provided a detailed framework for classification of wetlands of the central and south coast of California for the Environmental Protection Agency. Gordon and White (1994), Fites (1993), Smith (1994) and other USDA Forest Service ecologists have intensively sampled plant community diversity on their forests to provide fundamental information for improving communication between diverse resource specialists as well as providing eco-

logical information on potential community responses to management.

The oak woodlands of California have been of particular interest to ecologists and managers over the past 15 years. Political awareness arose out of perceived threats to the oak woodland from urban development, wood cutting, lack of oak regeneration and recruitment, and livestock grazing (Muick and Bartolome 1987; Bolsinger 1988). In a political response, a research, extension, and management program was forged; the Integrated Hardwood Range Management Program (IHRMP) was developed to direct and fund research and extension activities in California's oak woodlands (Passof and Bartolome 1985). The IHRMP has supported a number of studies on oak ecology, oak woodland ecology and management, wildlife, invertebrates, regeneration and recently water quality (Swiecki and Bernhardt 1991; Allen-Diaz and Holzman 1993; Davis et al. 1995; Campbell and Allen-Diaz 1997; Allen-Diaz et al. 1998; Allen-Diaz and Jackson 2000).

A concern of many government water quality agencies and private conservation groups are livestock effects on wetland and riparian systems. Predicting the effects of livestock grazing on riparian areas such as spring-fed wetlands remains elusive (Clary 1995; Larsen et al. 1998; Belsky et al. 1999; Clary 1999; Rinne 1999; Allen-Diaz and Jackson 2000). These systems respond to grazing treatments
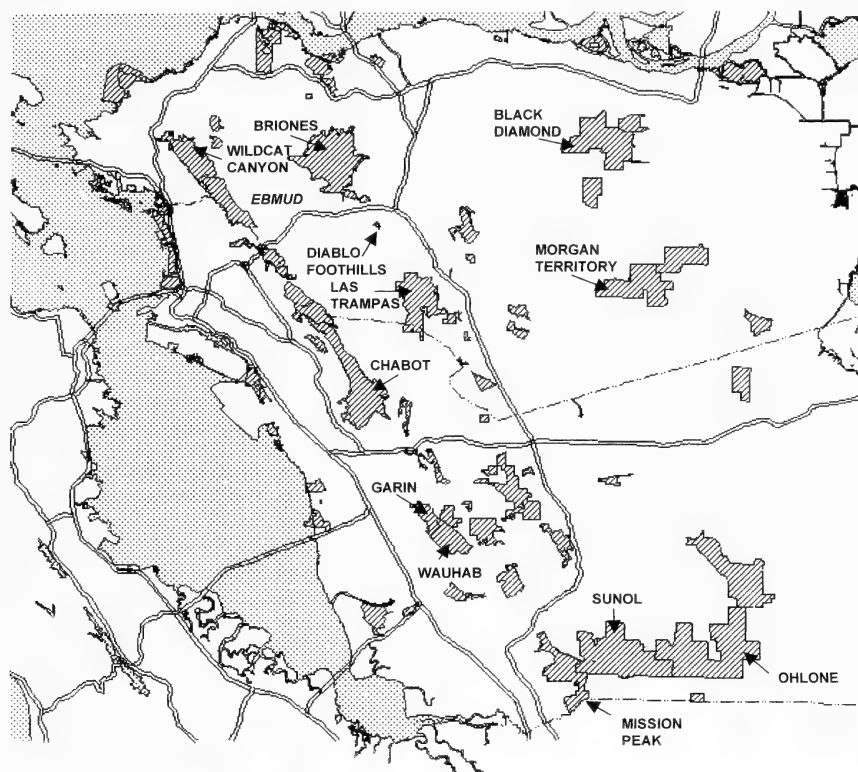
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FIG. 1.   East Bay Regional Parks and East Bay Municipal Utility District areas where springs were located.

in ways that do not always correspond with anecdotal and observational evidence (Kauffman and Krueger 1984). Disparity among results may lie in: 1) the confounding of grazing histories and other land-uses both past and present, 2) the application of grazing treatment levels that are not reflective of actual livestock use, 3) ambiguous or vague grazing system definitions, intensities, and seasons, 4) characteristics inherent to riparian ecosystems (i.e., non-equilibrium or chaotic dynamics), and/or 5) averaging of variability from site-specific responses. It follows that adequate description and understanding of riparian areas is lacking.

Nonetheless, management mandates abound. The 1987 renewal of the 1977 Clean Water Act amendment to the Federal Water Pollution Control Act of 1972 (PL 92-500; 33 U.S.C. s/s 1251 et seq.) shifted nonpoint-source pollution control emphasis from "direct threat to human health or safety" to "threat to ecosystems and habitat" (Sec 319). Revision of the Coastal Zone Management Act of 1992 (as amended by PL 92-583; 16 U.S.C. 1451 et seq.) required states to develop and implement nonpoint-source pollution programs and establish management measures for implementation. Moyle et al. (1996) contains appendices listing riparian protection guidelines and prescriptions on federal and private lands.

The East Bay Regional Park District (EBRPD) has recently conducted hearings to collect public and expert input to guide future management on park landscapes. Hence, we sought coarse-scale patterns that might indicate whether community types at spring-fed ecosystems were influenced by the presence or absence of livestock grazing. Toward this end, we described and classified spring-fed plant community types on the hardwood rangelands of California's East Bay Hills and then related these vegetation types to environmental and management factors. These results should inform future survey stratification and experimental design.

STUDY SITES

The East Bay Municipal Utility District (EB-MUD) owns and manages approximately 11,330 ha in the East Bay (Fig. 1). EBMUD's reservoirs store high-quality drinking water for approximately 1.2 million users. Domestic livestock grazing has been a significant component on these rangelands for at least 100 years. At the time of this study, cattle were managed on 7285 ha, with 22,000 AUM's (animal unit months) grazed annually (EBMUD 1995).

The EBRPD manages 36,834 ha (20,457 ha in Alameda County; 16,377 ha in Contra Costa County) in 50 regional parks (EBRPD 1996). In 1992, about 15,785 ha were leased to grazing cattle for an authorized use of 24,000 AUM's (EBRPD 1992). Ungrazed spring sites were determined by

TABLE 1. EAST BAY REGIONAL PARK DISTRICT AND EAST BAY MUNICIPAL UTILITY DISTRICT SAMPLING SITES. [1] Number of sites.

Site	Grazed	Ungrazed	[1]Means of grazing exclusion
EBRPD			
Black Diamond	2	0	
Briones	7	0	
Chabot	0	1	fence
Diablo Foothills	1	0	
Garin	1	1	fence
Las Trampas	2	2	topography (2)
Mission Peak	3	2	fence (2)
Morgan Territory	6	1	fence
Ohlone	4	0	
Sunol	2	3	fence (2), topography (1)
Wauhab	2	0	
Wildcat Canyon	10	2	fence (1), topography (1)
EBMUD			
North	11	1	fence
South	4	0	
Totals	55	13	

assessing their physical accessibility (fences, shrub cover, topography) and evidence of livestock absence (no fecal material, untrampled soil, ungrazed vegetation). Specific dates of livestock exclusion were not available, but all fencing material had apparently aged substantially and exclusion by shrubs and topography would have existed for decades to millennia (or at least as long as the development of the spring itself).

The goals of the EBMUD and EBRPD livestock grazing programs are to manage livestock in order to maintain and enhance the health of the grassland ecosystem, remove fuels where fire poses a significant hazard, maintain a healthy agricultural economy where consistent with other district goals, protect and enhance water quality, and generate revenue (EBRPD 1992, EBMUD 1995).

FIG. 2. Spring site sampling schematic.

Spring head

10-m diameter shrub and overstory sampling plot

10-m line-point herbaceous vegetation transects

METHODS

Data were collected March through June of 1991 and 1992 from 68 (55 grazed and 13 ungrazed) spring sites (Table 1). Sites were found by locating them on 7.5″ quadrangle topographic maps. Sites were then visited and selected if vegetation indicated an active spring and no recent disturbance to develop the spring for livestock use was evident. Sampled sites included those maintaining old weir boxes (indicating past development) but exhibiting established vegetation, as well as springs that had apparently never been developed.

A sharp ecotone was present between spring vegetation and surrounding upland areas, which allowed for point-source designation along the upslope boundary, i.e., the point from which water flowed. Where weir boxes had been previously installed, the downslope side of the spring box or pond was considered the point-source.

Elevation, aspect, slope, slope position, and soil parameters were estimated for each site. Vegetation data were collected from two 10-m point-intercept transects (Bonham 1989) run parallel to streamflow and emanating from a randomly located point on either side of the spring head but confined to the "green zone" delineating spring vegetation (Fig. 2). Herbaceous plant species that were intercepted by a sharpened point lowered at 10 cm intervals along each transect were recorded for a total of 200 point-observations per site. A 5-m radius circular plot centered on the spring head was used to ocularly estimate relative cover of trees and shrubs. Bias and measurement error were minimized by ensuring that all plots in each year were estimated by a single individual (Elzinga et al. 1998). The difficulty of ocular estimation of cover increases with the number of taxa present (Elzinga et al. 1998),
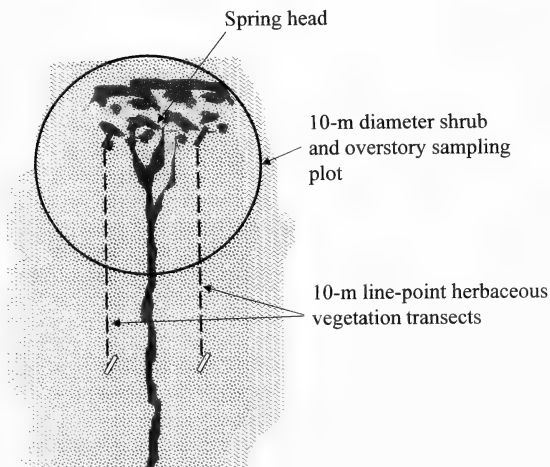
however most of our plots were dominated by only two or three tree and/or shrub species. Fine-scale differences in these vegetation layers by species combinations were not instrumental in the subsequent classification. Unknown species were collected and keyed to species using Munz and Keck (1973) and then updated according to Hickman (1993).

We delineated plant communities by subjecting the combined herbaceous, shrub, and tree layer cover data to the classification software TWINSPAN (PC-ORD version 4, Hill 1979; McCune and Mefford 1999). TWINSPAN uses cover classes delimited according to cut-levels that specify class ranges. Default cut-levels were used resulting in absolute cover classes of >0 to 2%, 3 to 5%, 6 to 10%, 11 to 20%, and >20%. TWINSPAN uses each cover class x species combination to create pseudospecies, e.g., *Bromus hordeaceus* L. 6–10% is considered a different taxon than *B. hordeaceus* 11–20%. Pseudospecies are then used to drive a divisive classification, each level of which is the result of bifurcating groups produced by previous divisions. The relative strength of a division, hence the resultant 2 groups, was denoted by an eigenvalue (λ) showing increasing strength from 0.00 to 1.00 (Gauch 1982). Eigenvalues approximate the percentage of pseudospecies not common to each group, so, $\lambda = 1$ denotes 2 groups with no pseudospecies overlap (Jongman et al. 1995). Eigenvalues provide an objective criterion for determining the merit of each division, although, the λ at which further splits are ignored (the critical λ) is a subjective choice dependent on the research question. We sought a relatively broad scale classification so $\lambda = 0.30$ was used as our critical λ.

Canonical correspondence analysis (CCA, PC-ORD version 4, McCune and Mefford 1999; Ter Braak 1986; Ter Braak 1987) was employed to relate environmental and management factors to the vegetative groupings determined with TWINSPAN. CCA finds the linear combination of these factors that maximizes species dispersion along an ordination or canonical axis. As with TWINSPAN, the strength of this dispersion is indicated by an eigenvalue (λ). The correlation of environmental variables to canonical axes was assessed by examining intraset correlations (Palmer 1993). The correlation matrix of environmental variables indicated no multicollinearity problems. Monte Carlo tests of significance were run with 99 iterations for each canonical axis.

Three of the 68 sites were eliminated from the CCA analysis because they contained missing values. Eight environmental variables were entered into the CCA. The variable ASPECT was created by taking the absolute value of 180 minus the azimuth reading resulting in values ranging from 0 for south and 180 for north (*sensu* Stohlgren et al. 2000). Only 3 textural classes were evident at these sites: loam, clay loam, and clay. Hence, binary dummy variables were created as LOAM or CLAY-LOAM with all other sites classified as CLAY. The presence or absence of livestock grazing was also coded as a binary dummy variable (GRAZED). The remaining variables were continuous: ELEVATION (m), SLOPE (%), LITTER (% cover of all dead organic matter), and BARE (% cover of bare ground).

Finally, DCA (PC-ORD version 4, McCune and Mefford 1999) was performed on the species matrix to assess the ability of CCA-generated ordination axes to depict important underlying gradients. DCA extracts ordination axes from the species matrix as does CCA, but DCA ordination is not constrained by specified environmental variables. DCA simply maximizes species dispersion using a 2-way weighted averaging algorithm (Jongman et al. 1995). Hence, DCA provides some indication of the total amount of dispersion or variability in a species matrix, while CCA shows how a combination of environmental or management variables can emulate this dispersion. If DCA and CCA generate gradients of similar magnitude (i.e., $\lambda_{DCA} \approx \lambda_{CCA}$) we would conclude that the environmental variables provide a *well-specified* model of gradients in the species matrix. Conversely, an *under-specified* CCA model is one where the combination of environmental and management variables do not approximate gradients generated from the species matrix alone (i.e., $\lambda_{DCA} \gg \lambda_{CCA}$). In practice, λ_{DCA} will always be greater than λ_{CCA}, so comparisons must remain qualitative and used in an exploratory manner as we have done here. A distinction must be made between using these ordination techniques for testing hypotheses (i.e., where manipulations of treatment variables are made) and for exploring structure or pattern in a dataset. A rigorous experimental design would include *a priori* grazing contrasts that were randomly assigned to each site. In this case, a balanced design where equal numbers of grazed and ungrazed sites were sampled would be ideal. However, ours was a heuristic use of ordination to search for possible relationships between environmental and management variables and community types and to examine how sites were distributed along these gradients. Our unbalanced design (more grazed than ungrazed sites) does not affect this technique because it was not an experimental design, but an exploratory analysis.

RESULTS

A total of 207 plant species were found on the springs, including 16 trees and 4 shrubs. Four oak species were found at the springs, coast live oak (*Quercus agrifolia* Nee), valley oak (*Q. lobata* Nee), blue oak (*Q. douglasii* Hook. & Arn.), and interior live oak (*Q. wislizeni* A. DC.). In addition, willow (*Salix* spp.) and California bay (*Umbellularia californica* [Hook. & Arn.] Nutt.), and sometimes alder (*Alnus rhombifolia* Nutt.), California

TABLE 2. SYNOPTIC TABLE FROM TWINSPAN CLASSIFICATION. Values indicate pseudospecies cover classes, i.e., (1) T–2%, (2) 3–5%, (3) 6–10%, (4) 11–20%, (5) >20%. Taxa are categorized by vertical vegetation layers, i.e., (o) = overstory, (s) = shrub, (h) = herbaceous.

Community type →	Ryegrass-herbaceous																																				Rush-herbaceous								Willow-Poison oak										California bay-Poison oak										
Site code →	1604	1104	0901	0204	1781	2009	2083	1901	2902	1103	3001	2603	1905	1709	1681	1601	1225	1221	1220	1106	1102	1101	0281	1906	1219	1107	0313	3001	3086	3084	3082	1707	1113	1114	2084	1111	1304	1605	3081	3002	3081	3010	3005	1112	1903	3083	1704	1109	3002	0318	0316	1306	3003	1105	1981	1908	2981	1904	0301	0385	0381	0504	2001	1716	0383

Taxa

(Taxa rows, with vegetation layer in parentheses)

- sedges
- common rush
- American speedwell
- bog rush
- iris-leaved rush
- common monkeyflower
- watercress
- ryegrass
- soft chess
- toad rush
- ripgut brome
- horsetail
- moss
- coast live oak (o)
- California bay (o)
- California bay (h)
- blackberry (h)
- poison oak (s)
- poison oak (h)
- willow (o)
- willow (h)
- blackberry (s)

TABLE 3. RYEGRASS-HERBACEOUS TYPE DESCRIPTIVE STATISTICS. Constancy equals the number of species occurrences/ total number of plots; cover equals the mean cover (%) of a species for a given type; and range equals the range of cover values (T = trace or <1%).

		Con-stancy	Cover	Range
Characteristic plant taxa				
Lolium multiflorum Lam.	ryegrass	94	12	T–44
Juncus bufonius L.	toad rush	69	4	T–22
Rorippa nasturium-aqutica (L.) Hayek	watercress	67	6	T–39
Polypogon monspeliensis (L.) Desf.	rabbitfoot grass	44	3	T–33
Bromus diandrus Roth	ripgut brome	44	1	T–8
Juncus xiphioides E. Meyer	iris-leaved rush	39	4	T–31
Bromus hordeaceus L.	soft chess	36	1	T–7
Mimulus guttatus DC.	common monkeyflower	31	2	T–29
Geranium molle L.	common geranium	28	1	T–4
Hordeum marinum Hudson	Mediterranean barley	28	1	T–10
Juncus effusus L.	bog rush	28	10	1–29
moss	moss	28	T	T–1
Biotic environment				
Total Vegetative Cover (%)	71 (35–100)			
Tree Cover (%)	49 (1–100) n = 14			
Shrub Cover (%)	13 (1–50) n = 13			
Grass Cover (%)	43 (1–85) n = 36			
Forb Cover (%)	13 (1–65) n = 36			
Abiotic environment				
Elevation (m)	376 (128–817)			
Slope (%)	21 (0–65)			
Aspect	SW primarily			
Position	Mid-slope, upper/lower slopes, draws			
Bare (%)	25 (1–62) n = 36			
Rock (%)	5 (1–21) n = 20			
Soil Series	Los Osos, various			
Texture	Clay loam, sandy clay loam, loam			
Coarse Fragments (%)	22 (1–60) n = 14			
Rootability	Hard & massive, hard & fractured			
Soil Drainage	Somewhat-poorly to poorly drained			

buckeye (*Aesculus californica* [Spach] Nutt.), or big-leaf maple (*Acer macrophyllum* Pursh), were common on springs with a tree overstory. Willows were identified to genus because of poor catkin years.

Spring herbaceous species were diverse and were significant in identifying spring types. No rare, threatened or endangered species were identified in the spring samples.

Spring plant communities. We identified 4 plant community types for the East Bay Hills oak woodlands (Table 2). The initial split by TWINSPAN divided the tree-dominated *types* from the herbaceous-dominated plots (λ = 0.608). The herbaceous *types* were distinguished from one another based on the amount of sedges (*Carex* spp.), rushes (*Juncus* spp.), and horsetail (*Equisetum arvense* L.) present, all indicative of wetter sites (λ = 0.418). Two tree-dominated types were distinguished when TWIN-SPAN separated California bay from willow sites (λ = 0.531).

Ryegrass-herbaceous type.—The Ryegrass-herbaceous type (Table 3) was dominated by ryegrass

(*Lolium multiflorum* Lam.), watercress (*Rorippa nasturium-aquaticum* [L.] Hayek), and toad rush (*Juncus bufonius* L.). This type averaged 43% total grass cover and 13% total forb cover. Total vegetation cover averaged 71%, ranging between 35% and 100% cover (herbaceous + shrubs + trees). Only 39% of the springs in this type maintained a tree overstory, and only 36% of the plots in this type maintained a shrub component.

Elevation averaged 376 m (128–817 m), textural classes were primarily somewhat poorly drained clay loams. Thirty-three of the 36 sample springs in the Ryegrass-herbaceous type were grazed by cattle.

Rush-herbaceous type.—The Rush-herbaceous type (Table 4) was characterized by the presence of two rush species: common rush (*Juncus patens* E. Meyer) and *J. xiphioides* E. Meyer. Ryegrass was still a common component, and willows occurred on about 5 of the 11 plots in the type. Sedges (*Carex* spp.), American speedwell (*Veronica americana* [Raf.] Benth.), and field horsetail (*Equisetum avense* L.) also occurred frequently. The Rush-her-

TABLE 4. RUSH-HERBACEOUS TYPE DESCRIPTIVE STATISTICS. Constancy equals the number of species occurrences/total number of plots; cover equals the mean cover (%) of a species for a given type (T = trace or <1%); and range equals the range of cover values.

		Con-stancy	Cover	Range
Characteristic plant taxa				
Salix spp.	willow	45	46	1–100
Rhamnus californica Eschsch.	California coffeeberry	27	14	3–24
Rubus ursinus Cham. & Schldl.	California blackberry	55	10	5–15
Lolium multiflorum Lam.	ryegrass	73	3	T–8
Juncus patens E. Meyer	common rush	73	3	T–10
Juncus xiphoides E. Meyer	iris-leaved rush	73	5	T–16
Veronica americana (Raf.) Benth	American speedwell	64	6	2–14
Carex spp.	sedge	64	7	2–16
Equisetum arvense L.	field horsetail	55	17	T–35
Juncus effusus L.	bog rush	45	8	3–14
Mimulus guttatus DC.	common monkeyflower	45	5	1–18
Conium maculatum L.	poison hemlock	36	3	2–6
Juncus bufonius L.	toad rush	36	1	T–3
Rorippa nasturium-aquatica (L.) Hayek	watercress	27	4	2–6
Picris echioides L.	bristly oxtongue	27	1	T–2
Bromus diandrus Roth	ripgut brome	27	4	2–8
Cynara cardunculus L.	artichoke thistle	27	9	5–14
Biotic environment				
Total Vegetative Cover (%)	83 (55–100)			
Tree Cover (%)	57 (1–100) n = 8			
Shrub Cover (%)	22 (1–57) n = 8			
Grass Cover (%)	29 (10–50) n = 10			
Forb Cover (%)	22 (1–65) n = 11			
Abiotic environment				
Elevation (m)	253 (128–402)			
Slope (%)	21 (10–32)			
Aspect	NW primarily			
Position	Upper and mid slopes, draws			
Bare (%)	19 (3–50) n = 10			
Rock (%)	3 (2–4) n = 2			
Soil Series	Los Gatos primarily			
Texture	Loams			
Coarse Fragments (%)	11 (4–15) n = 3			
Rootability	Hard & massive, hard & fractured			
Soil Drainage	Somewhat well to poorly drained			

baceous spring type was distinguished from the Ryegrass-herbaceous type by the presence of sedges and horsetail, as well as the occurrence of California blackberry (*Rubus ursinus* Cham. & Schldl.) and/or a woody overstory. Total vegetation cover averaged 83%, which is similar to the Ryegrass-herbaceous type. Tree and/or shrub cover was found on this type about 73% of the time, and when found, averaged 57% and 22% cover, respectively.

The Rush-herbaceous type was found at an average elevation of 253 m (128–402 m) on loamy textured soils. Three of the 11 plots classified as Rush-herbaceous were ungrazed.

Willow-Poison oak type.—The Willow-Poison oak type (Table 5) was dominated by willows. On plots without willow, blue elderberry (*Sambucus mexicana* C. Presl) was often present. Poison oak (*Toxicodendron diversilobum* [Torrey & A. Gray] E. Greene) was common, occurring on 73% of the

11 sample plots classified in this type. The herbaceous understory was sparse with total graminoid cover averaging 19%, and forb cover averaging 8%. Shrub cover averaged 40% and was found on all plots classified in this type. Tree cover averaged 49% and occurred on all but one plot in this type where the shrub coffeeberry (*Rhamnus californica* Eschsch.) was found.

The Willow-Poison oak type occurred on sites averaging 254 m (116–536 m) elevation. Soils were predominantly loams, and 5 of 11 sites in this type were ungrazed.

California bay-Poison oak type.—The California bay-Poison oak type (Table 6) was dominated by California bay. Coast live oak was present as the overstory species at the one site in this type that did not contain California bay. This type also contained Poison oak, blackberry, mosses, and occasionally chainfern (*Woodwardia fimbriata* Smith).

TABLE 5. WILLOW-POISON OAK TYPE DESCRIPTIVE STATISTICS. Constancy equals the number of species occurrences/ total number of plots; cover equals the mean cover (%) of a species for a given type; and range equals the range of cover values (T = trace or <1%).

		Constancy	Cover	Range
Characteristic plant taxa				
Salix spp.	willow	73	42	25–56
Sambucus mexicana C. Presl	blue elderberry	27	9	4–18
Toxicodendron diversilobum (Torrey & A. Gray) E. Greene	poison oak	73	26	1–64
Baccharis pilularis DC.	baccharis	45	20	T–59
Rubus ursinus Cham. & Schldl.	California blackberry	45	23	2–60
Lolium multiflorum Lam.	ryegrass	36	2	T–4
Bromus diandrus Roth	ripgut brome	27	7	3–13
Carex spp.	sedge	27	2	T–3
Biotic environment				
Total Vegetative Cover (%)	85 (50–95)			
Tree Cover (%)	49 (5–93) n = 10			
Shrub Cover (%)	40 (5–80) n = 11			
Grass Cover (%)	19 (1–50) n = 11			
Forb Cover (%)	8 (1–35) n = 11			
Abiotic environment				
Elevation (m)	286 (116–536)			
Slope (%)	21 (5–58)			
Aspect	SE, SW			
Position	Upper, mid, lower slopes			
Bare (%)	33 (5–60) n = 10			
Rock (%)	14 (1–20) n = 3			
Soil Series	Los Osos, various			
Texture	Loams			
Coarse Fragments (%)	19 (1–60) n = 4			
Rootability	Primarily hard & massive			
Soil Drainage	Primarily well drained			

Total vegetation cover averaged 91%. Graminoid and forb cover was very low, 5% and 11% respectively. Tree cover averaged 83% and was found on all plots in this type. Seventy-five percent of the plots in this type maintained shrub cover which averaged 32% when present.

Elevation ranges for this type were 122 to 658 m with an average of 394 m. Grazing occurred at two of the 12 sites in this type. The textural class of these soils was primarily loams.

Environmental and management factors. CCA ordination axes showed that at least 3 significant orthogonal gradients could be created by taking the linear combination of environmental variables (Table 7). Axis 1 (CCA$_1$) was most closely correlated with the variable LITTER. The California bay-Poison oak type scored high on this vector compared to the other 3 vegetation groups (Fig. 3a).

CCA$_2$ was correlated with ELEVATION primarily; however, the two categorical variables LOAM and CLAYLOAM were also useful in creating this axis (Table 7). Though CCA$_2$ helped disperse the species matrix as a whole, indicating a strong underlying gradient, it provided minimal insight into the separation of vegetation types. Willow-Poison oak sites generally scored positively while the

Rush-herbaceous type appeared at mainly below-average elevations.

Finally, CCA$_3$ separated sites within all four vegetation types (Figs. 3b, c) apparently for the presence or absence of grazing (Table 7). However, only 2 California bay-Poison oak sites scored positively (indicating no grazing) on CCA$_3$ (Fig. 3c), contrasting CCA$_2$ and CCA$_3$.

Three DCA axes were also extracted from the species matrix whose very high eigenvalues indicated 3 underlying gradients that were not completely explained by linear combinations of our environmental and management variables, i.e., DCA found even stronger gradients than CCA (Table 7). This indicated an under-specified explanatory model for this species matrix. Classical indirect gradient analysis would continue from this point by inferring causes of these gradients. Figure 4a shows that DCA$_1$ arrays our TWINSPAN-derived vegetation groupings from overstory to herbaceous types with little overlap, while DCA$_2$ separates the higher-elevation California bay-Poison oak sites from the middle-elevation Willow-Poison oak and Ryegrass-herbaceous types. Rush-herbaceous sites tended to be located at lower elevations, which is also reflected in Figure 4a. There is no evidence from Figures

TABLE 6. CALIFORNIA BAY-POISON OAK TYPE DESCRIPTIVE STATISTICS. Constancy equals the number of species occurrences/total number of plots; cover equals the mean cover (%) of a species for a given type; and range equals the range of cover values (T = trace or <1%).

		Constancy	Cover	Range
Characteristic plant taxa				
Umbellularia californica (Hook. & Arn.) Nutt.	California bay	92	57	16–100
Quercus agrifolia Nee	coast live oak	50	44	10–95
Acer macrophyllum Pursh	big leaf maple	25	17	1–32
Toxicodendron diversilobum (Torrey & A. Gray) E. Greene	poison oak	75	23	T–20
Rubus ursinus Cham. & Schldl.	California blackberry	42	6	3–17
moss	moss	42	4	1–17
Galium aparine L.	common bedstraw	25	1	T–3
Woodwardia fimbriata Smith	chainfern	25	11	4–25
Biotic environment				
Total Vegetative Cover (%)	91 (75–100)			
Tree Cover (%)	83 (45–100) n = 12			
Shrub Cover (%)	32 (1–60) n = 9			
Grass Cover (%)	5 (1–15) n = 10			
Forb Cover (%)	14 (1–40) n = 11			
Abiotic environment				
Elevation (m)	394 (122–658)			
Slope (%)	30 (10–65)			
Aspect	All			
Position	Upper, mid, lower slopes			
Bare (%)	27 (7–65) n = 12			
Rock (%)	3 (2–7) n = 6			
Soil Series	Los Osos, various			
Texture	Loams			
Coarse Fragments (%)	34 (20–60) n = 4			
Rootability	Primarily fractured			
Soil Drainage	Excessively well to poorly drained			

4b and 3c that DCA_3 is a grazing gradient as determined for CCA_3 based on its high correlation with GRAZED. Caution must be used when interpreting correlations between ordination axes and binary variates. Hence we examined a scatterplot of grazed and ungrazed sites distributed along DCA_3

TABLE 7. ORDINATION RESULTS. [1] 180–azimuth.

	Axis 1	Axis 2	Axis 3
CCA Results			
Eigenvalue (λ)	0.487	0.415	0.363
P	0.02	0.01	0.01
Intraset correlations			
ELEVATION	−0.312	−0.554	−0.436
ASPECT[1]	−0.156	0.486	−0.221
SLOPE	−0.342	−0.207	−0.018
LOAM	−0.416	−0.445	0.341
CLAYLOAM	0.321	0.428	−0.579
LITTER	−0.834	0.062	0.156
BARE	−0.211	0.276	−0.153
GRAZING	0.192	−0.006	−0.852
DCA Results			
Eigenvalue (λ)	0.765	0.636	0.547

that showed the fewer number of ungrazed sites to be randomly distributed with a narrow range among the many grazed sites that exhibited a much wider range of distribution along DCA_3 (Fig. 5).

Figure 6 shows selected taxa arrayed along CCA_2 and CCA_3. The dotted line indicates where in species space ungrazed sites were found vis-à-vis grazed sites; there was no overlap. Overstory willows (oSALIX), blackberry shrub (sRUUR), and herbaceous layer Poison oak (hTODI) scored highly on CCA_3 concomitant with ungrazed plots. While willows were also found on the grazed plots, they tended to be found as sSALIX—willows in a shrub state. Other overstory taxa were found on grazed plots as California bay (oUMCA) and Coast live oak (oQUAG). Herbaceous taxa were distributed along the negative side of the CCA_3 axis with Italian ryegrass (hLOMU) and common monkeyflower (hMIGU) scoring highest for grazed plots and sedges (hCAREX) and rushes (hJUXI, hJUEF) scoring moderately.

DISCUSSION

DCA axes displayed three much stronger underlying gradients than CCA axes exposed, making it
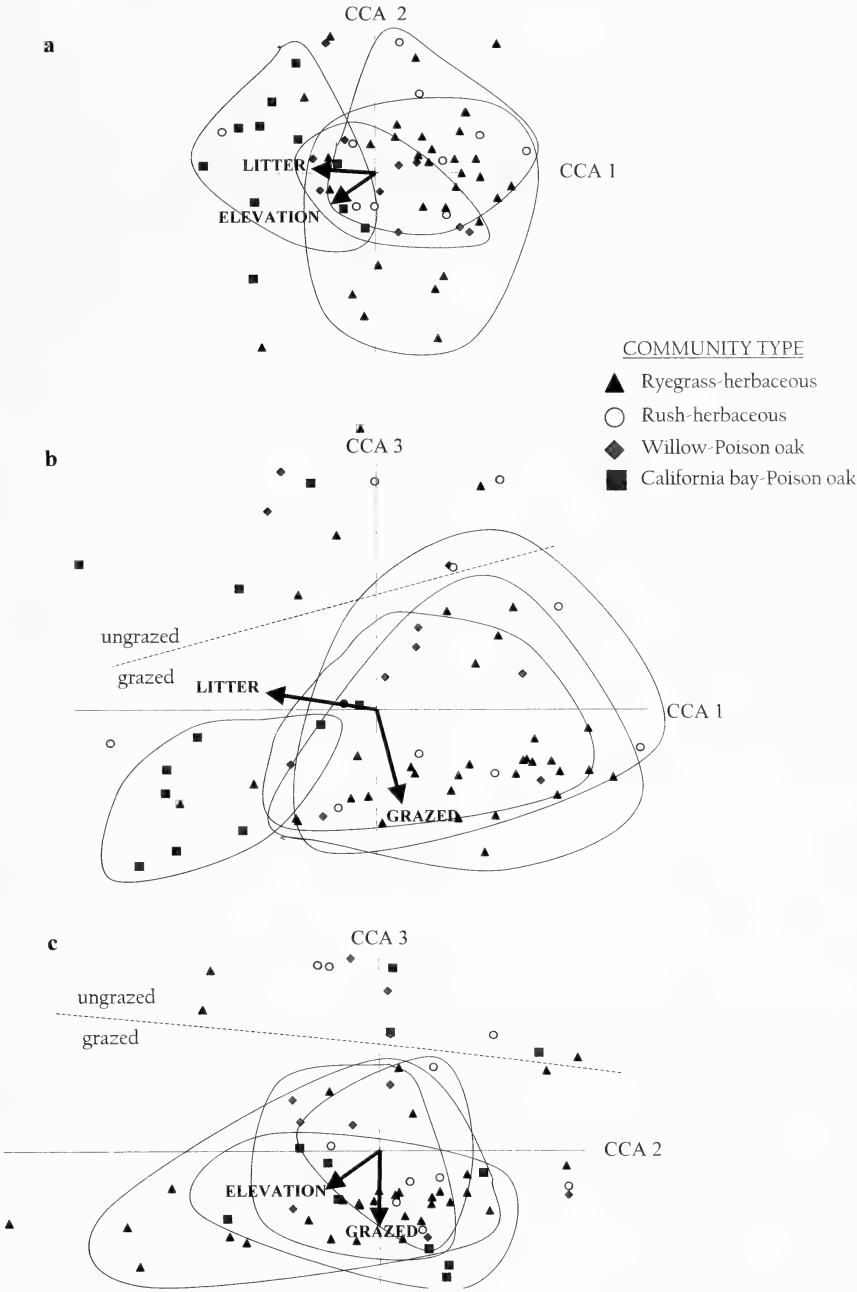
FIG. 3.   Canonical correspondence analysis (CCA) joint-plots contrasting each of 3 orthogonal ordination axes. All sites above dotted line were ungrazed; all sites below were grazed. Note: polygons not inclusive of all sites from a given community type.

clear that the CCA model was under-specified, i.e., one or more driving factors were not included. CCA_1's correlation with litter quantity indicated a productivity gradient from the relatively low-productivity annual grass-dominated Ryegrass-herbaceous type to the high biomass tree types—California bay-Poison oak and Willow-Poison oak. This spread seems indicative of a gradient driven by water availability. Ryegrass is an annual species that

fares well on dry uplands as well as on areas that undergo periodic inundation throughout California, while rushes tend to be hydrophilic taxa existing in topographic depressions, seeps, and springs (Bowerman 1944; Keator 1994). At lower elevation spring sites, water availability is likely to be more constant than at higher elevation sites due to greater upslope catchment area. Hence, these lower elevation sites with even greater water availability and
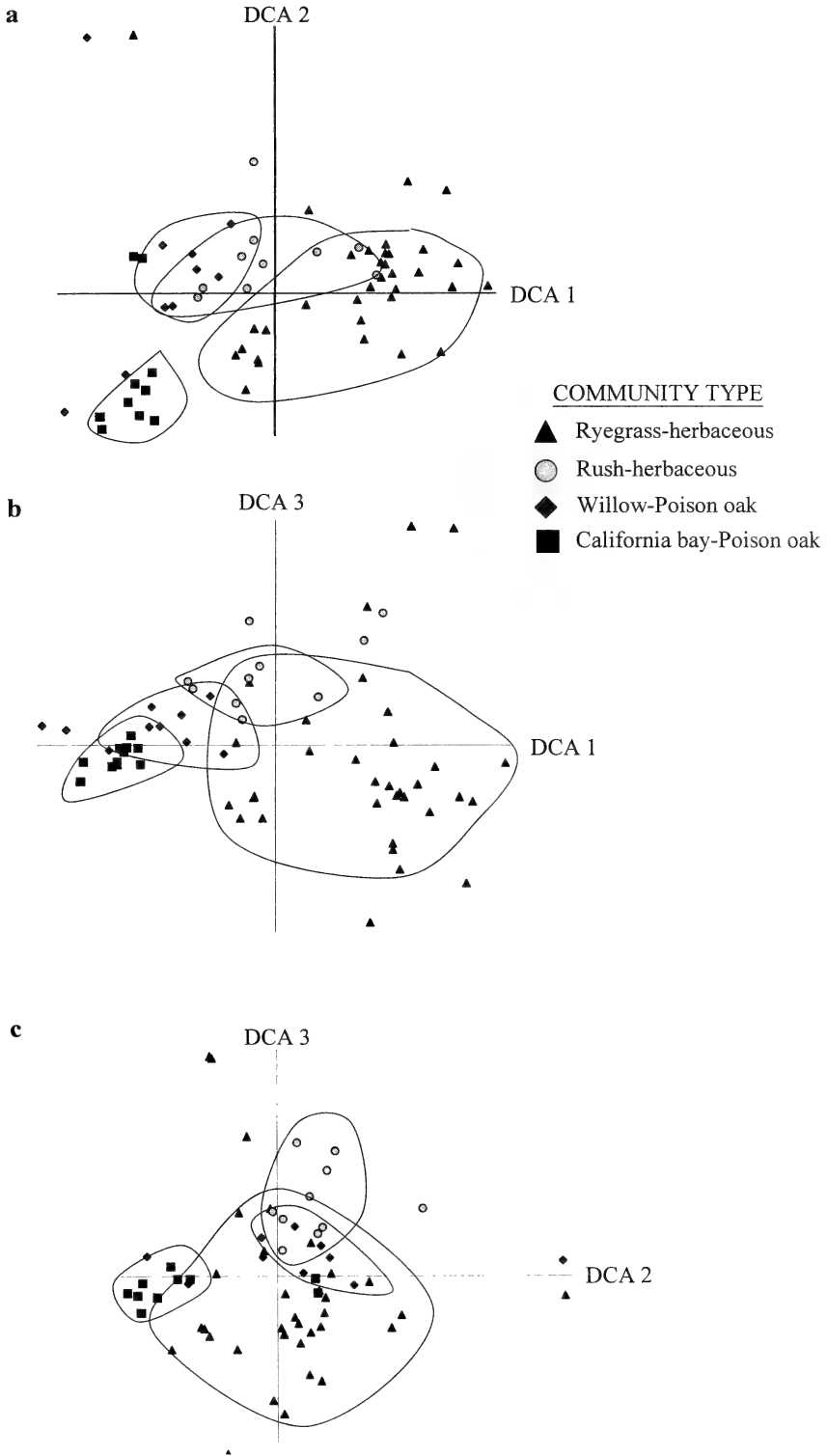
FIG. 4. Detrended correspondence analysis (DCA) joint-plots contrasting each of 3 orthogonal ordination axes. Note: polygons not inclusive of all sites from a given community type.
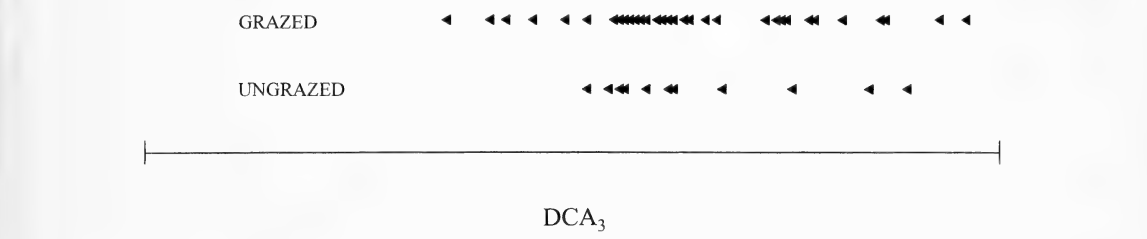
FIG. 5.   Distribution of ungrazed and grazed sites along the third detrended correspondence analysis gradient (DCA₃).

probably higher flows support willows. Willows are known to use stream water in addition to soil water to compete effectively with herbaceous vegetation, which uses soil water only (Alstad et al. 1999). Finally, it was not surprising that the California bay-Poison oak type scored high for greater litter levels since California bay is known for recalcitrant, slowly decomposing leaves-due to its relatively high concentrations of phenolic secondary compounds, (Goralka and Langenheim 1995). California bay-Poison oak sites also often maintained a coffeeberry or blackberry shrub component adding to the high productivity.

CCA₂ indicated a strong gradient, orthogonal to the productivity gradient discussed above (CCA₁), that appeared tied to elevational differences among sites. However, the categorical soil texture variables LOAM and CLAYLOAM each showed high correlations with CCA₂ as well. Visual examination of Figures 3a and 3c showed that while CCA₂ strongly separated some of the individual species, it did not disperse our four plant groupings very well. Perhaps some species wax and wane with temperature fluctuations that vary with elevation while the dominant taxa (which defined the vegetation types) re-

main. Also, the coarseness of our soil texture variables may play a role in the relative ambiguity of the gradient represented by CCA₂.

The correlation coefficients for LOAM and CLAYLOAM showed opposite signs with respect to CCA₂. LOAM corresponded roughly to higher elevations and CLAYLOAM to lower sites indicative of greater soil weathering via periodic inundation.

CCA₃ appeared to represent a species ordination related to the presence or absence of livestock grazing. Interestingly, three plots from each type were ungrazed and all scored highly on CCA₃ indicating that these sites all had something in common vegetatively. A popular notion is that livestock grazing degrades riparian areas and especially remove the willow component. The presence of willow at both grazed and ungrazed sites argues against this notion at first glance. Of the ten sites classified as Willow-Poison oak, six were grazed. What seems clear from Figure 6 is that while willows were present at both grazed and ungrazed sites, their size-classes were likely affected so that grazed sites maintained more of a willow shrub component, while ungrazed sites were more likely to maintain willows in the
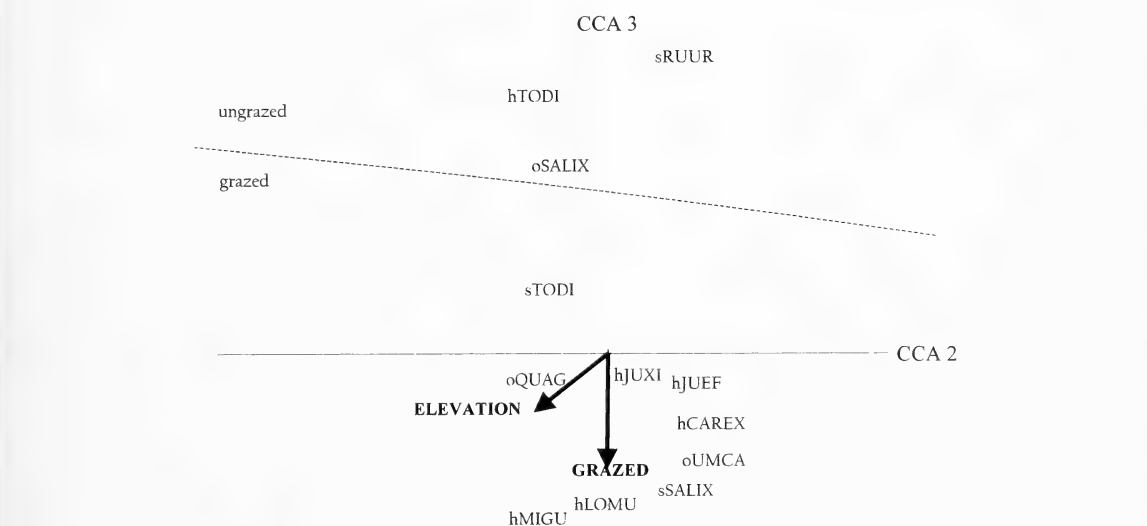
FIG. 6.   Canonical correspondence analysis (CCA) joint-plot (same as Figure 3c) showing selected taxa with associated vertical layer prefix, i.e., herbaceous (h), shrub (s), or overstory (o). Taxa are: RUUR—*Rubus ursinus,* TODI—*Toxicodendron diversiloba,* SALIX—*Salix* spp., QUAG—*Quercus agrifolia,* JUXI—*Juncus xiphioides,* JUEF—*J. effusus,* CAREX—*Carex* spp., UMCA—*Umbellularia california,* MIGU—*Mimulus guttatus,* LOMU—*Lolium multiflorum.*

overstory. These results align with Peinetti et al. (2001) who showed willow productivity was unaffected by large herbivores, but that overall morphology shifted to more prostrate growth forms with grazing. They further concluded that the temporal distribution of grazing was important in determining these effects.

Another conspicuous pattern emerging from the 4 ungrazed Willow-Poison oak sites was the high cover of blackberry in the shrub layer (often >40% cover) and the herbaceous layer (~5–20% cover). We have also observed the conversion of herbaceous spring sites to blackberry shrub dominance that completely eliminates the herbaceous component at Sierra Nevada oak woodland springs (B. Allen-Diaz unpublished data).

Interestingly, both the Ryegrass-herbaceous and the California bay-Poison oak types scored positively for grazing (negatively on CCA_3) showing that both life-form types (herbaceous and overstory) were extant under this management scenario. More detailed information about grazing management (intensity and temporal distribution) under experimental designs needs to be applied before conclusions about grazing effects on spring types can be verified. Livestock grazing has been implicated in general riparian area degradation (Fleischner 1994; Belsky et al. 1999), but has also received credit for ameliorating streambank slumping (Myers and Swanson 1992) and freshwater fish habitat (Knapp et al. 1998). Allen-Diaz and Jackson (2000) showed that light to moderate grazing intensity (based on upland residual dry matter estimates) resulted no compositional shifts on Sierra Nevada oak woodland springs. Certainly, overgrazing (unsustainable grazing pressure), will induce a cascade of deleterious effects on ecosystems, i.e., bank erosion, vegetation loss, reduced stream water quality (Belsky et al. 1999), however, there is neither casual nor scientific indication that either of the two land management agencies discussed here practice overgrazing.

Grazing presence/absence does not appear to influence the community type overall (i.e., composition) but may have important within-type effects on the vegetative structure when willows are present. Other overstory taxa did not show this pattern.

By using quantitative, quasi-objective classification analysis, we were able to delimit four spring-fed plant community types for the East Bay Hills, California. Finer scale description would certainly provide a greater number of community types; these four appeared to repeat strongly across these landscapes. These results should not be taken as evidence that livestock grazing has no important effects on these systems—only well designed field experiments will inform these questions. However, these results should provide useful information to those designing and implementing future experiments and surveys. Other California landscapes and regions containing similar and disparate spring

types also need delineation. For instance, we did not observe the ubiquitous cattail type (*Typha* spp.) so often observed in Sierra Nevada foothill oak woodlands. Community types should be described on a site-specific basis in order to more fully characterize variability within and among these patch ecosystems.

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ATRIPLEX ROBUSTA (CHENOPODIACEAE), A NEW PERENNIAL SPECIES FROM NORTHWESTERN UTAH

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Abstract

Atriplex robusta is a newly described species from northwestern Utah. It is abundant along the shoulders of roads and highways and in slightly elevated terrain within and bordering saline playas. It appears to be morphologically closest to *A. tridentata* Kuntze but differs in its larger stature, more woody, caespitose habit, larger urn-shaped fruiting bracts and broader leaves.

On the shoulders of Highway I-80 between Grantsville and Wendover, Tooele County, Utah in northwestern Utah, there are numerous small populations of a distinctive form of perennial *Atriplex*. Because of its robust habit we refer to it as *A. robusta,* described below as a new species. It is particularly abundant about 65 km east of Wendover near the railroad siding at Knolls. In this area *Atriplex canescens* (Pursh) Nutt. and *A. tridentata* Kuntze come together, hybridize and produce a variety of hybrid segregants including plants of *A. robusta* which appear to have spread, as a new species, for several miles along the freeway (I-80) shoulders, in both directions.

Atriplex robusta H. C. Stutz, M. R. Stutz, and S. C. Sanderson, sp. nov. (Fig. 1).—TYPE: USA, Utah, Tooele Co., 1 mi W of Knolls, T15 R13W S15, shoulder of highway I-80, 1280 m elevation, 16 Sep 1977, *H. C. Stutz 8141* (Holotype: BRY; Isotypes, BRY, CA, CAS, GH, MO, NY, RM, UC).

Frutices caespitosi, 40–80 cm alti. Caules erecti vel ascendentes, ramosi a basi ad apicem, dense furfuraceus, 1–8 mm diam., fragilis. Folia oblonga, ascendentia usque appressa, dense furfuracea; folia ephemera verna et aestiva 15–30 mm longa, 5–10 mm lata; folia serotina aestiva et hiberna 3–10 mm longa, 2–5 mm lata, anatomia foliaris Kranz-typi. Plantae dioeciae, raro monoeciae. Flores staminati sessiles, ad brevi-ramulus axillares in angustipaniculas terminales; perianthium campanulatum, 5-partitum ad medium, dense furfuraceum, segmentis ovatis usque ellipticis, 2 mm longis, 1 mm latis; stamina 5, filamentis 1 mm longis, antheris ca. 2 mm longis, 1 mm latis. Flores pistilati solitarii, sessiles, in plerumque sine foliis confertas paniculas terminales. Bracteae fructiferae furfuraceae, compressae, urceolatae, latissimae infra media, 5 mm latae, 7–8 mm longae, exappendiculatae, cum 3–10 marginalibus dentibus, 0.5–2 mm longis, qui medianus longissimus. Utriculus orbiculatus, pericarpio membranceo pellucido. Semena 5 mm diam., testa membranacea, brunnea; radicula supera.

Perennial caespitose shrub, 40–80 cm tall (Fig. 2). Stems erect or ascending, ramified from base to top, densely furfuraceous, 1–8 mm in diameter, brittle. Leaves oblong, obtuse, ascending to appressed, densely furfuraceous, Kranz-type anatomy, ephemeral spring and summer leaves 5–10 mm wide, 15–30 mm long, late summer and winter leaves 2–5 mm wide, 3–10 mm long. Plants dioecious, rarely monoecious; staminate flowers sessile, on short axillary branches in terminal narrow panicles, calyx campanulate, sepals 5, united halfway, densely scurfy, ovate to elliptical, 1 mm wide, 2 mm long, stamens 5, yellow, filaments 1 mm long, anthers 2 mm long, 1 mm wide; pistillate flowers solitary, sessile, in dense, mostly non-leafy, terminal panicles, bracteoles furfuraceous, laterally compressed, urceolate, widest below the middle, 5 mm wide, 7–8 mm long, unappendaged, united to near the apical margin, marginal lips slightly divergent, marginal teeth 3–10, conspicuous, 0.5–2 mm long, central tooth largest. Utricles orbicular, pericarp membranaceous, transparent. Seeds 5 mm in diameter, testa membranaceous, brown, radicle superior. Flowering period: June–July. Chromosome number: $2n = 54$.

Additional Collections: USA, Utah, Tooele Co.: road shoulder W of Knolls, 30 Apr 1975, *K. Harper;* shoulders of highway I-80, Knolls, T15 R13W S15, 25 Sep 1975, *H.C. Stutz 7842;* Knolls, 26 Jul 1977, *H.C. Stutz 8068;* 1 mi S of Knolls, T15 R13W S23, 17 Aug 1978, *H.C. Stutz 8338;* 8 mi W of Knolls, T15 R14W S16, 12 Jul 1979, *H.C. Stutz 8461;* 3 mi W of Knolls on shoulders of old abandoned highway, T15 R13W S21, 20 Sep 1994, *H.C. Stutz 9670;* 1 mi W of Knolls on old highway, 9 Sep 1995, *H.C. Stutz 9831.*

FIG. 1. *Atriplex robusta*. a. Habit. b. Fruiting bract. c. Seed. (Illustrations by Loretta Orgill.)

Atriplex robusta is common in Tooele county, Utah, particularly along the shoulders of Highway I-80 (Fig. 3). Its nearest relative appears to be *A. tridentata* Kuntze, from which it differs in several significant features. The fruiting bracts of *A. robusta* usually have trident or polydent apical margins like those in most *A. tridentata* plants, but they are considerably larger (5 mm wide × 6–8 mm long vs. 3 mm wide × 4 mm long). The fruiting bracts of *A. robusta* are urn-shaped, non-appendaged, whereas those of *A. tridentata* are cuneate and usually appendaged. *A. robusta* plants are much taller than *A. tridentata* (40–80 cm vs. 20–50 cm) and woodier, and in contrast to *A. tridentata* plants, *A.*

robusta plants do not form root-sprouts. The leaves of *A. robusta* are much wider than those of *A. tridentata* (5–10 mm vs. 2–5 mm). *Atriplex robusta* differs from *A. canescens* in its non-winged fruiting bracts, more herbaceous habit, smaller stature, broader leaves and urn-shaped utricles.

Associated Species. The principal associates of *A. robusta* are *Allenrolfea occidentalis* (Wats.) Kuntze and *Suaeda torreyana* Wats. Each of these species appears to be well adapted to the conditions along the shoulders of the roads and railroads in these areas. *Allenrolfea* and *Suaeda* plants also occur in some abundance in many of the surrounding saline playas, but *A. robusta* appears to be mostly restricted to the limited habitat along the shoulders of roadways that provides increased amounts of fresh water and improved leaching of salts, and in elevated areas within the saline playas. Near Knolls, where a sizeable population of *A. canescens* occurs, hybrids between *A. robusta* and *A. canescens* are common. Although *A. robusta* is hexaploid and the putative *A. canescens* parent is tetraploid, the resulting pentaploid hybrids are partially fertile and segregant progeny, displaying a wide array of intermediate phenotypes, are fairly common.

A POSSIBLE ORIGIN OF *ATRIPLEX ROBUSTA*

As reported by Stutz et al. (1979), *A. robusta* appears to have been derived from hybrids between tetraploid *A. canescens* ($2n = 36$) and hexaploid *A. tridentata* ($2n = 54$). Near Knolls, Tooele C., Utah, where *A. robusta* is abundant, both *A. canescens* and *A. tridentata* are present, as well as putative hybrids between them and also several plants that appear to be segregants from the hybrids including plants described as *A. robusta*. In this area, *A. canescens* is abundant on sand dunes that extend to the south shoulder of Highway I-80 and a few *A. tridentata* plants are on the adjacent lower, saline flats. Sizeable populations of *A. tridentata* occur a few miles to the east and a few miles to the west, on bottomland clay soils.

The contrast in phenotypes of *A. canescens, A. tridentata* and *A. robusta* plants in this area, is striking. *Atriplex canescens* plants are tall (1–2 meters), caespitose, woody shrubs with large leaves (ca. 5 mm wide × 30 mm long), and large 4-winged fruiting bracts (20 × 20 mm). *Atriplex tridentata* plants are short (ca. 20–50 cm), herbaceous, subshrubs with vigorous root sprouts, and leaves that are mostly small and linear (ca. 5 × 20 mm). *Atriplex robusta* plants are intermediate, in several features supporting the conjecture that it is a derivative from *A. tridentata* × *A. canescens* hybrids. They are larger-statured (40–80 cm) than *A. tridentata* plants and smaller than those of *A. canescens,* more woody than *A. tridentata* plants, less woody than *A. canescens* plants and their distinctive, mostly smooth surfaced, urn-shaped fruiting bracts are much larger than those of *A. tridentata* and smaller

FIG. 2.   *Atriplex robusta.* A single plant in a population near Knolls, Tooele Co., Utah. Bar = 30 cm.

FIG. 3.   Population of *Atriplex robusta,* near Knolls, Tooele Co., Utah. Bar = 80 cm for plants in foreground.

than those of *A. canescens.* Collectively, their caespitose habit, intermediate stature, large, broad, obtuse leaves, numerous upright stems and large, unappendaged, urn-shaped fruiting bracts, clearly set *A. robusta* plants apart from those of both putative parents.

Hybrids between *A. tridentata* and *A. canescens* are common whenever they occur together in nature, and although such hybrids are highly sterile pentaploids, fertile derivatives are sometimes derived from them (Stutz et al. 1979; Stutz and Sanderson 1998). Since, at Knolls, there is a large population of *A. canescens,* but only a few *A. tridentata* plants where the hybrids and hybrid derivatives are common, *A. tridentata* plants were probably the female parents of the hybrids. Their relative scarcity may have enhanced the production of hybrid offspring.

If this interpretation of the origin of *A. robusta* is correct, *A. robusta* is probably of rather recent vintage because its preferred habitat, along the shoulders of Highway I-80 and neighboring roadways, is also very young (I-80 was completed in 1969). An early count of *A. robusta* plants on the shoulders of the west-bound lane of I-80 near Knolls, in 1975, by the authors, showed approximately 17,500 plants on the shoulders of the west-bound lanes. Assuming the same density on the shoulders of the east-bound lanes, there were approximately 35,000 plants present in 1975; today there appear to be millions. Their rapid increase was probably enhanced by their high seed production; some individual plants produce more than 25,000 fruits.

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A NEW *IPOMOPSIS* (PALE MONIACEAE) FROM THE SOUTHWEST USA AND ADJACENT MEXICO

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Abstract

Ipomopsis longiflora subsp. **neomexicana,** a new subspecies, is distinguished from subsp. *longiflora* (Torr.) V. E. Grant and subsp. *australis* R. A. Fletcher and W. L. Wagner by its annual habit, ovaries with a modal number of 30 ovules, minutely winged seeds, and ellipsoid capsules that are about twice the length of the calyces. Subspecies *neomexicana* occurs in parts of the Great Basin and Chihuahuan Desert, ranging from southeastern Utah and southern Colorado through eastern Arizona and New Mexico into northern Mexico. The 3 subspecies are self-compatible, strongly self-pollinating, but have flowers that attract hawkmoths.

Ipomopsis longiflora (Torr.) V. E. Grant is based on a specimen (Holotype: NY!) collected by Edwin James "on the Canadian River," probably what is now the North Canadian River in Oklahoma (McKelvey 1956). Descriptions of *Ipomopsis longiflora* were given by Wilken (1986), Welsh et al. (1987), and Cronquist et al. (1984), the latter two under the name *Gilia longiflora* (Torr.) G. Don. The species is distinguished from all members of *Ipomopsis* by its sparsely glandular-puberulent herbage, pinnatifid leaves with 5–7 linear to narrowly oblong segments, open, paniculate inflorescences, glandular-puberulent calyx tubes, and white to pale blue salverform corollas that are 25–45 mm long. *Ipomopsis longiflora* is confused sometimes with the related *I. laxiflora* (J. M. Coult.) V. E. Grant, which has a smaller stature and corolla tubes between 8 and 20 mm long (Wilken 1986). Subspecies *longiflora* is a biennial of the western Great Plains, distributed from South Dakota to central Texas (Wilken 1986). It is characterized by narrowly ellipsoid capsules that are about the length of the calyx.

Fletcher and Wagner (1984) applied the name *I. longiflora* subsp. *australis* to plants with ovoid or broadly ellipsoid capsules that are equal to or that only slightly exceed the calyx. Fletcher and Wagner also reported differences in seed shape and calyx lobe vestiture. Subspecies *australis* occurs from "Mohave Co., Arizona, south and west of the Mogollon Plateau, to southwestern New Mexico as far east as Deming in Luna Co., New Mexico, and to northern Sonora" (Fletcher and Wagner 1984). However, Fletcher and Wagner did not study specimens of the species east of the Rocky Mountains. While reviewing specimens and conducting field work for the Flora of the Great Plains and Flora of North America projects, I noticed differences between plants of the Great Plains and those treated as subsp. *longiflora* by Fletcher and Wagner. Plants from the Great Plains are all assignable to the typ-

ical subspecies, but plants referred to subsp. *longiflora* by Fletcher and Wagner are recognized here as a new, morphologically and geographically distinct subspecies.

Ipomopsis longiflora (Torr.) V. E. Grant subsp. **neomexicana** Wilken, subsp. nov. (Fig. 1)— TYPE: USA, New Mexico: Sierra Co., Mitchell Point Road, 1.6 mi N of junction with Interstate 25, 14 mi N of Truth or Consequences. 15 May 1985, *Wilken 14323* (Holotype UNM; isotypes ARIZ, CAS, CS, RM, RSA, UC).

Herba annua foliosa, 20–52 cm alta. Folia caulina pinnatifida, 12–35 cm longa, supra glabri infra secus costas sparsim pubescentes; partes 5–7, anguste lineares, laterales distantes 5–19 mm longae, terminales 9–29 mm longa. Inflorescentia laxa subcorymbosa vel aliquantum rotundata; bracteae simplices vel subulatae, 7–15 mm longae. Calyces in statu florendi 6–9 mm longae, extus minute glandulosus, interne prope apices loborum puberulus. Corollae hypocrateriformes, 30–47 mm longae; lobis late obovatis vel rotundati, persaepe caesii, 7–10 mm longi. Capsulae ellipsoidae, 10–15 mm longae, calyce 1.5–2plo longiorae. Semina anguste ellipsoidea, pallide flavo-brunea, 2.5–3 mm longa, ad apices minute alati.

Annual herb 20–52 cm tall, with one to four erect to ascending branches arising from below middle of central axis. *Stems* glabrous to sparsely invested with short, uniseriate, eglandular and glandular trichomes. *Leaves* 12–35 mm long, pinnatifid, with (3)5–7(9) linear segments ca. 1–2 mm wide, lateral segments 5–19 mm long, distal segments 9–29 mm long, petioles 4–13 mm long; basal leaves in a rosette, senescent at anthesis; cauline leaves 18–35 mm long, gradually reduced upwards, subglabrous above, sometimes with minute trichomes bearing a terminal, globose cell, sparsely pubescent on lower surface of rachis and lateral segments, trichomes uniseriate and mostly eglandular. *Inflores-*
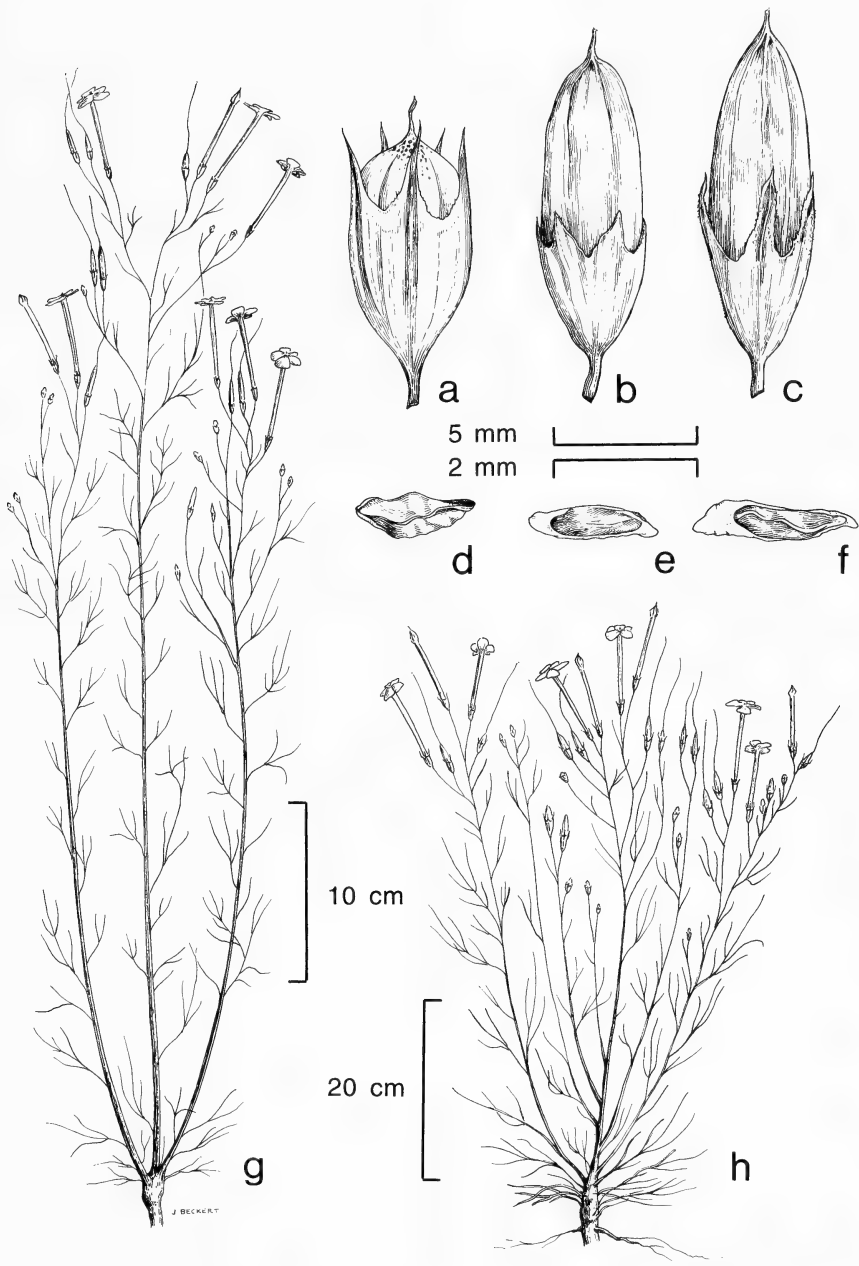
FIG. 1.   *Ipomopsis longiflora*, with details of diagnostic characters that separate the subspecies. A-C. Calyx and fruit. A. ssp. *australis*. B. ssp. *neomexicana* C. ssp. *longiflora*. D-F. Seeds. D. ssp. *australis*. E. ssp. *neomexicana* F. ssp. *longiflora*. G. Generalized habit of ssp. *longiflora*. H. Generalized habit of ssp. *neomexicana*.

cences indeterminate, paniculate, corymbiform to somewhat rounded, with flowers in loose, terminal clusters of 2–3; bracts simple, linear to aculeate, 7–15 mm long; pedicels slender, 9–24 (30) mm long, sparsely glandular-puberulent, trichomes uniseriate with a terminal globose cell. *Calyces* 6–9 mm long, tube 3–6 mm long, lobes 2.5–4 mm long, narrowly acuminate, tube sparsely to moderately glandular-puberulent externally, lobe apices eglandular puberulent within, trichomes uniseriate and straight or slightly curled. *Corollas* salverform, 30–47 mm long, glabrous, tube white, lobes elliptic to subrotund, 7–10 mm long, usually pale bluish or bluish lavender, sometimes white, apices rounded to apiculate. *Ovary* 5–6 mm long, style 25–44 mm long, stigmas included in the tube, sometimes slightly exserted, stigmatic branches 2–3 mm long; ovules 8–10 per locule. *Stamens* inserted unequally above mid-tube, 3–4 included, 1–2 slightly exserted, lower filaments subsessile to 4 mm long, upper fila-

ments 1–3 mm long, anthers 2–3 mm long. *Pollen* white, sometimes bluish, grains subspheroidal, zonocolporate, colpi 6–8, exine striate or striate-reticulate near colpi. *Capsules* 10–15 mm long, 1.5–2 times longer than the fruiting calyx; seeds 2.5–3 mm long, yellowish brown, narrowly ellipsoid, dorsal margins and apices minutely winged.

Paratypes. USA, Arizona: Apache Co., 10 mi N of Springerville, *Pase 1508* 31 Aug 1965 (ASU), Coconino Co., Flagstaff, *Hanson 128* 11 Jun 1922 (LL, NY, TX), Mohave Co., Mociac Ranch, *Cottam 4171* 6 Jun 1929 (NY), Navajo Co., 5 mi N of Snowflake, *Deaver 6490* 12 Jul 1963 (ARIZ, ASU), Yavapai Co., Cornville, *Jones 266* 19 Sep 1922 (ARIZ); Colorado: Alamosa Co., 25 mi NE of Alamosa, *Iltis 4352* 11 Jul 1953 (RSA, WI), Costilla Co., N of Alamosa, *Bethel, Willey & Clokey 4250* 27 Jun 1921 (NY, POM, RM, US, WS), La Plata Co., Animas River, 2 mi S of Bondad, *Ownbey 1445* 17 Aug 1937 (NY, RM, UTC, WS), Montezuma Co., McElmo Canyon, *Weber 7948* 1 Sep 1952 (COLO, WS), Montrose Co., La Sal Creek, *Gierisch 1381* 21 Jun 1942 (RM), Saguache Co., Crestone, *Ramaley 12089* 18 Jul 1928 (RM); New Mexico, Bernalillo Co., Rio Puerco, *Ripley & Barneby 2379* 7 Oct 1939 (NY), Catron Co., E of Reserve, *Clark s.n.* 17 Aug 1942 (UNM), Doña Ana Co., 3 mi E of Las Cruces, *Ward 66* 9 Apr 1981 (LL, NMC, NY, TX), Eddy Co., 22 mi SW of Carlsbad, *Waterfall 3750* 14 Aug 1942 (NY), Grant Co., 8 mi W of Silver City, *Barkley 14694* 24 Sep 1944 (OKL), Guadalupe Co., 1 mi E of Santa Rosa, *Clark 10016* 18 Jun 1951 (UNM), Lincoln Co., 4 mi NW of Capitan, *Stephens 25897* 29 Jul 1968 (KANU), Luna Co., 5 mi S of Deming, *Sands s.n.* 6 Jun 1962 (UNM), McKinley Co., 7 mi NE of Borrego Pass, *Marley 1575* 21 Jun 1978 (UNM), Otero Co., 11 mi W of Cloudcroft, *Waterfall 12951* 22 Aug 1956 (ARIZ, US), Rio Arriba Co., near Española, *Correll 50851* 26 Jul 1979 (NY), San Juan Co., 4 mi N of La Plata, *Spellenberg & Ward 6155* 11 Aug 1981 (NMC), Sandoval Co., 12 mi N of San Ysido, *Shultz & Shultz 1304* (NY, UTC), Santa Fe Co., 13 mi W of Pojoaque, *Gentry 23037* 6 Sep 1972 (ASU), Socorro Co., 5 mi W of Bingham, *Dunn 5201* 6 Oct 1948 (UNM), Taos Co., Ojo Caliente, *Smith s.n.* 30 Jul 1894 (WS), Torrance Co., 8 mi S of Estancia, *Martin 4374* 12 Sep 1960 (UNM), Valencia Co., El Morro Nat. Mon., *Kayes 42* 9 Jul 1978 (UNM); Texas, Brewster Co.: 2 mi E of Lajitas, *Higgins 2763* 25 May 1970 (NY), Culberson Co., near Van Horn, *Warnock 388* 20 Apr 1938 (TX), El Paso Co., Hueco Tanks, *Powell & Powell 3005* 12 Jul 1976 (TX), Hudspeth Co., 8 mi W of Sierra Blanca, *Hitchcock 6775* 25 Jun 1940 (NY, POM, UTC, WS), Presidio Co., 11 mi S of Marfa, *Correll & Rollins 23651* 19 Apr 1961 (NY TX); Utah, Garfield Co., 11.4 mi E of Escalante, *Holmgren & Holmgren 4719* 10 Aug 1970 (KANU, NY, US, UTC), Grand Co., Dead Horse Point, *Car-*

TABLE 1. COLLECTION DATA FOR CHROMOSOME COUNTS AND PHENOLOGY STUDIES OF *IPOMOPSIS LONGIFLORA*. Voucher specimens for chromosome counts are deposited at CS unless otherwise noted.

Subsp. *longiflora*. Colorado, Logan Co., US Highway 6, 2.8 mi E of junction with Interstate 76, 29 Sep 1982, *Wilken 13887*, $2n = 14$; Nebraska, Sheridan Co., 0.8 mi N of Niobrara River, 12 Aug 1983. *Wilken 13988*, $2n = 14$.

Subsp. *neomexicana*. Arizona, Apache Co., Hwy 666, 2 mi N of Zuni Wash, 21 May 1985, *Wilken 14422*, $2n = 14$, Coconino Co., between Wupatki Ruin and Sunset Crater, 8 Aug 1987, *Wilken 14844*, $2n = 14$; Colorado, Alamosa Co., 5 mi E of Alamosa, 7 Jul 1986, *O'Kane 2464*; New Mexico, Sierra Co., Mitchell Point Rd, 1.6 mi N of junction with Interstate 25, 15 May 1985, *Wilken 14323*, $2n = 14$; Texas, El Paso Co., El Paso, 28 Mar 1983, *Worthington 9651* $2n = 14$, (UTEP).

Subsp. *australis*. Arizona, Gila Co., Hwy 60, N side of Gila River Bridge, 21 May 1985, *Wilken 14416*, $2n = 14$, Hwy 77, 12 mi N of Globe, 20 May 1985, *Wilken 14414*, $2n = 14$.

ter 1561 27 May 1940 (UTC), San Juan Co., near La Sal, *Flowers 2084* 7 Jun 1939 (NY). MEXICO, Chihuahua, 4.8 mi S of Samalayuca, *Hendrickson 5783* 19 Aug 1971 (TX), Coahuila, 10 mi s of Laguna del Rey, *Hendrickson 14158* 20 Sep 1974 (TX).

METHODS

677 specimens from 21 herbaria were studied (ARIZ, ASU, BRY, COLO, CS, KANU, KSU, LL, NEB, NMC, NY, OKL, POM, RM, RSA, TX, UNM, US, UTC, WI, WS). Eight quantitative characters were chosen for detailed study (Table 2). Measurements were made on a subset of specimens that represented the geographic range of each taxon. Sample sizes for each character varied, depending on the condition of specimens. Field studies were conducted in one to three populations of each subspecies (Table 1) to study population structure and to obtain seeds for assessing life history characteristics under controlled conditions, the breeding system, and chromosome number. Seeds were germinated in a greenhouse at Colorado State University, Fort Collins, Colorado in late November and transplanted to 6-inch diameter pots in early January. Plants of subsp. *australis* and subsp. *neomexicana*, which began bolting in March, completed their life cycles (April–May) under greenhouse conditions. Plants of subsp. *longiflora* continued to produce basal leaves throughout the spring and early summer months, but did not flower. Ten plants from each of two populations were retained under greenhouse conditions; a total of 21 additional plants were transplanted to a garden in July. Self-compatibility and autogamous seed production relative to manipulative self-pollination were assessed in plants by enclosing inflorescences in loose-fitting bags constructed from cheesecloth. Self-compati-

TABLE 2. COMPARATIVE TABLE OF DIAGNOSTIC CHARACTERS OF *IPOMOPSIS LONGIFLORA* SUBSPECIES. The mean, standard deviation, and sample size (in parentheses) are given for each quantitative character. Midcauline leaf segment number and number of ovules per ovary are reported as modes, followed by range and sample size in parentheses.

Character	*I. l. australis*	*I. l. longiflora*	*I. l. neomexicana*
Plant height (cm)	24.1 ± 9.4 (45)	61.0 ± 15.6 (71)	24.9 ± 9.3 (83)
Basal stem diameter (mm)	2.6 ± 0.1 (45)	7.0 ± 0.2 (71)	2.8 ± 0.1 (83)
Midcauline leaf segment number	5 (3–7; 51)	7 (5–9; 71)	5 (3–7; 93)
Midcauline leaf length (mm)	26.7 ± 7.3 (51)	37.6 ± 7.0 (71)	23.5 ± 5.8 (93)
Calyx lobe length (mm)	3.1 ± 0.7 (28)	2.1 ± 0.3 (32)	3.3 ± 0.5 (32)
Calyx lobe apex (internal) pubescence	dense	glabrous to sparse	moderate to dense
Modal ovule number	24 (17–24; 50)	30 (22–30; 50)	30 (23–30; 50)
Capsule length (mm)	8.8 ± 1.1 (30)	11.8 ± 1.5 (34)	12.5 ± 1.7 (36)
Capsule length/fruiting calyx length	1.1 ± 0.1 (30)	1.8 ± 0.3 (34)	1.9 ± 0.1 (36)
Seed apex wing length (mm)	0.1 ± 0.0 (50)	0.3 ± 0.1 (50)	0.6 ± 0.2 (50)

bility was assessed by emasculating flower buds prior to anthesis and anther dehiscence and directly applying pollen to stigmas using dehisced anthers from the same plant. Flowers were also permitted to complete anthesis without manipulation. Mature capsules were dissected and the number of seeds in each and counted (Table 3). The ovary of a third flower on the same plant was dissected to estimate ovule number. Chromosome counts were made by studying actively growing root tips and flower buds, using orcein in proprionic acid (modified from Smith 1974).

MORPHOLOGICAL RELATIONSHIPS, CHROMOSOME NUMBER, AND DISTRIBUTION

Several diagnostic characters separate the three subspecies (Table 2). Plants of subsp. *longiflora* are generally more than twice as tall as those of subsp. *australis* and ssp. *neomexicana*. The lower 2–10 cm of the stems are thick, sclerified, and about twice as wide at the base than in either subsp. *australis* and subsp. *neomexicana*. Cauline leaves are longer and tend to have more segments. The lowest inflorescence branches in subsp. *longiflora* usually occur above the middle, whereas in most plants of subsp. *australis* and subsp. *neomexicana* they occur well below the middle (Fig. 1). Calyx lobe length in subsp. *australis* and subsp. *neomexicana* averages about 1 mm longer than in subsp. *longiflora*.

All three taxa have calyx lobes that are minutely glandular on the outer surface. However, the inner surfaces of lobe apices are moderately to densely eglandular puberulent in subsp. *australis* and subsp. *neomexicana*. Those of subsp. *longiflora* are either glabrous or bear only a few eglandular trichomes. Twenty-four ovules per ovary are modal in subsp. *australis*, as compared to 30 ovules in subsp. *longiflora* and subsp. *neomexicana* (Table 3). The fruits of subsp. *neomexicana* resemble those of subsp. *longiflora* in length and shape (Fig. 1; Table 3). Capsules are ellipsoid and about twice the length of the fruiting calyx in both taxa. Seeds of subsp. *longiflora* and *neomexicana* are narrowly ellipsoid, with a flat to slightly convex dorsal surface, and minutely winged along the margin and at the tips (Fig. 1). In subsp. *australis*, the capsules are ovoid to broadly ellipsoid, shorter in length, and scarcely exceed the calyx (Fig. 1; Table 2), and the seeds are essentially wingless (Fig. 1; Table 2).

The typical subspecies is a western Great Plains endemic, ranging from southwestern South Dakota (Bennett and Todd Cos.) south through western Nebraska, eastern Colorado, western Kansas, western Oklahoma, eastern New Mexico, and northwestern Texas (Fig. 2). It often occurs on sandy soils, especially sand hills in the northern plains and sandy alluvials along principal tributaries of the upper Niobrara, Platte, Republican, Arkansas, Canadian, Red, and Brazos rivers.

TABLE 3. COMPARISON OF AUTOGAMOUS VERSUS MANIPULATED SELF-POLLINATION IN *IPOMOPSIS LONGIFLORA*. Mean ovule number, mean seed number per capsule, and mean seed set, expressed as a proportion of ovule number, ± standard error. Sample size is uniformly 50 capsules.

	I. l. australis	*I. l. longiflora*	*I. l. neomexicana*
Ovule number			
Mean ovule number	19.8 ± 0.4	27.7 ± 0.4	26.1 ± 0.5
Autogamous self-pollination			
Mean seed number	11.3 ± 0.6	10.5 ± 0.9	13.1 ± 0.8
Seed/ovule ratio	57.8 ± 3.2	38.0 ± 3.8	50.4 ± 3.1
Manipulated self-pollination			
Mean seed number	15.7 ± 0.4	18.7 ± 0.4	19.7 ± 0.5
Seed/ovule ratio	80.1 ± 1.7	67.9 ± 1.5	76.1 ± 1.5
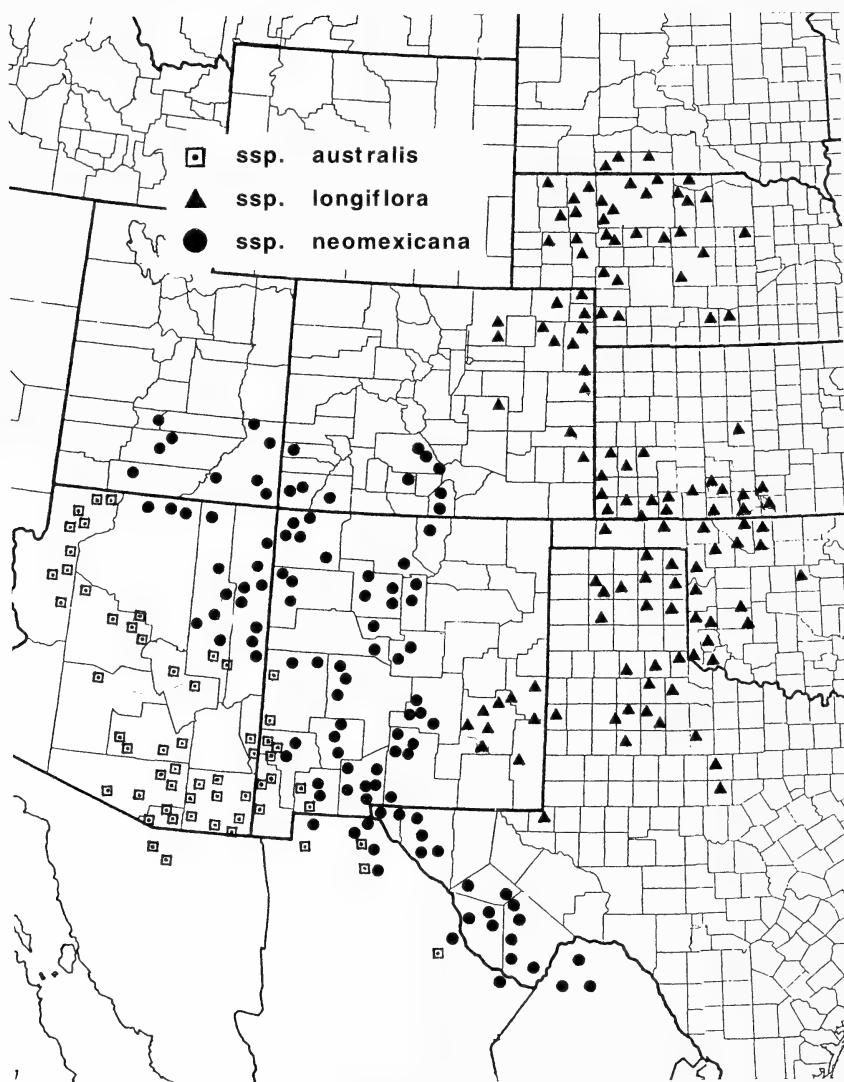
Fig. 2.   Geographic distribution of *Ipomopsis longiflora*.

The distribution of subsp. *australis* coincides with the northeastern portion of the Sonoran Subprovince, as defined by Thorne (1993). It occurs on sandy soils of open sites in desert shrublands, grasslands, and woodlands, generally south of the Mogollon Rim in Arizona, and extending south to Sonora and northwestern Chihuahua, Mexico (Fig. 2). Subspecies *neomexicana* occurs in similar habitats, but its distribution coincides with the southeastern Great Basin Province and Chihuahuan Subprovince (Thorne 1993). It occurs from southeastern Utah and southwestern Colorado, through eastern Arizona and New Mexico as far south as northern Coahuila. The distribution of each subspecies is largely allopatric, although some populations of subsp. *australis* and subsp. *neomexicana* are less than 40 km apart (Fig. 2; east-central Arizona,

southwestern New Mexico, and northern Chihuahua).

Grant (1959) reported $2n = 14$ for plants now treated as subsp. *longiflora* (Colorado, Weld Co., Grant 9503, RSA) and subsp. *neomexicana* (New Mexico, Socorro Co., Grant 8813, RSA). Additional counts of the same number were obtained from representative populations of each subspecies (Table 1).

VEGETATIVE AND REPRODUCTIVE BIOLOGY

Field and common garden studies suggest that subsp. *longiflora* is at least a biennial, whereas subsp. *australis* and *neomexicana* are annuals. Observations of subsp. *longiflora* in the sand hills of western Nebraska (Sheridan Co.) and eastern Colorado (Logan Co.) suggest that it lives through at

least two growing seasons, separated by one winter, prior to reproduction. Germination occurs during the spring (April–June) following snowmelt and late spring storms. Plants develop into vegetative rosettes that expand by additional growth during the first summer, remain dormant during the winter, followed by renewed rosette growth, shoot elongation, and reproduction during the late spring and summer months (May–September) of the second year. Plants grown to maturity from 6-month-old transplants in a common garden in Ft. Collins, Colorado required 18 months to flower. Plants grown under greenhouse conditions did not flower unless they were subjected to at least 10–12 weeks of cool, short-day conditions. In contrast, plants of subsp. *australis* and *neomexicana,* whose germination may coincide with either spring or summer monsoon precipitation, apparently complete their life cycle within 1 year. Plants of subsp. *australis* (north of Globe, Gila Co.) were recruited as seedlings during the spring and reproduced and died prior to the winter of the same year. Plants recruited during monsoon rains (July–August) over-wintered as rosettes and flowered in the succeeding spring and summer (March–September). Similar observations were made of subsp. *neomexicana* in the Rio Grande Valley of south-central Colorado (Alamosa Co.), northwestern Arizona (Apache and Coconino Cos.), and central New Mexico (Sierra Co.).

Ipomopsis longiflora is apparently pollinated by the hawkmoth, *Hyles lineata* (Grant and Grant 1965; Grant 1983). I observed unidentified hawkmoths in two populations (Table 1. subsp. *longiflora,* Logan Co., Colorado; subsp. *australis,* Gila Co., Arizona). *Hyles lineata* and *Manduca* were frequent visitors in experimental populations of all three taxa in Ft. Collins, Colorado. No other pollinator was observed on flowers of the three subspecies. Nectar is relatively high in sucrose, consistent with that expected in hawkmoth-pollinated flowers (Baker and Baker 1983; Freeman et al. 1985; Freeman and Wilken 1987).

Autogamous (unmanipulated) pollination resulted in seed/ovule ratios ranging from 38.0 in subsp. *longiflora* to 57.8 in subsp. *australis* and 50.4 in subsp. *neomexicana* (Table 3). Self-pollination of emasculated flowers resulted in seed/ovule ratios of 80.1 in subsp. *australis,* 67.9 in subsp. *longiflora,* and 76.1 in subsp. *neomexicana* (Table 3). These data provide further evidence of self-compatibility reported by Grant and Grant (1965) and suggest that *I. longiflora* may experience a mixed mating system favoring selfing, resulting from self-compatibility, close proximity of style branches and upper anthers, and pollination by hawkmoths.

KEY TO *IPOMOPSIS LAXIFLORA* AND THE SUBSPECIES OF *IPOMOPSIS LONGIFLORA*

1. Corolla tube 8–20 mm long, lobe 4–6 mm long; ovules 4–6 per locule . . . . *I. laxiflora*
1′ Corolla tube 25–45 mm long, lobe 6–11 mm long; ovules 6–10 per locule . . . . *I. longiflora*
2. Mature capsule ovoid to broadly ellipsoid, slightly exceeding the fruiting calyx; seed tip scarcely winged (wings < 0.1 mm long) . . . subsp. *australis*
2′ Mature capsule ellipsoid, about twice the length of the fruiting calyx; seed tip winged (wings > 0.2 mm long)
3. Inflorescence branches arising above the middle of the central axis; base of stem 4–9 mm in diameter; most cauline leaves with 7 segments . . . . subsp. *longiflora*
3′ Inflorescence branches arising from throughout central axis; base of stem 1–4 mm in diameter; most cauline leaves with 5 segments . . . . subsp. *neomexicana*

DISCUSSION

The three taxa comprising *Ipomopsis longiflora* share a combination of characters that are unique within the genus, including open, paniculate inflorescences, white to pale bluish, salverform corollas with tubes that exceed 20 mm in length, and pinnatifid leaves with 5–7 linear to narrowly oblong segments. Diagnostic differences among the three taxa are quantitative (Table 2), analogous to other infraspecific taxa within *Ipomopsis* (Grant and Wilken 1988). *Ipomopsis longiflora* ssp. *neomexicana* has no apparent autapomorphies and is separated by a combination of characters shared with either ssp. *australis* (e.g., habit, annual life form, inflorescence branching pattern, calyx and leaf morphology) or ssp. *longiflora* (ovule number, seed morphology, capsule length and shape). Its geographical distribution lies between that of the other subspecies. Other closely related taxa treated as species within *Ipomopsis* differ by one or more qualitative differences (e.g., leaf and inflorescence architecture, corolla morphology, anther position, filament length; see Grant 1959; Grant and Wilken 1988). Preliminary studies based on matK and ITS sequences show that the three taxa comprise a monophyletic lineage embedded within a largely unresolved polytomy of related taxa treated as species (M. Porter unpublished). Consequently, these taxa are treated as subspecies rather than as distinct species.

Like Fletcher and Wagner (1984) and Freeman et al. (1985), this study did not reveal any evidence of hybridization, parapatry (*sensu* Endler 1977), or intermediacy at the population level. Nectar-sugar composition, however, was significantly higher for sucrose in both subsp. *australis* and subsp. *neomexicana* populations near their "contact zone" in southwestern New Mexico (Freeman et al. 1985), suggesting some form of interaction. Although selection for increasing sucrose levels may be hypothesized as a consequence of gene flow, cross-compatibility among the three subspecies is unknown. Studies of the late Quaternary (Spaulding and Graumlich 1986; Van Devender et al. 1987; Wright 1976) suggest that the modern climate and

vegetation of the desert Southwest and western Great Plains developed during the last 10,000–15,000 years. Thus, the close relationships among the three subspecies and their distribution suggest a relatively recent origin and/or expansion of range, coincident with relatively rapid development of arid interior southwestern biomes.

Some populations of subsp. *australis* and subsp. *neomexicana* occur within 10–15 km of each other without apparent or significant differences in altitude, habitat, or vegetation. Notable areas of close proximity (Fig. 2) include the vicinities of Holbrook (Navajo Co., AZ) Silver City and Lordsburg (Grant Co., NM), and Samalyuca (northern Chihuahua, Mexico). Populations of subsp. *neomexicana* and subsp. *longiflora* occur within 30–40 km of each other in Chaves Co., NM. These potential contact zones may provide an opportunity to investigate the proximate causes of their respective distributions.

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A NEW SPECIES OF *POA* L. (POACEAE) FROM BAJA CALIFORNIA, MEXICO

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Abstract

A new perennial grass species, **Poa bajaensis,** is described from Baja California, Mexico. It is compared to *P. strictiramea* Hitchc, and the type of *P. orcuttiana* Vasey. The species has long been known by the latter name in herbaria. It may be distinguished from these by its short upper leaf blades, more closed sheaths, and abaxially smoother leaves and smoother panicle branches. It is endemic and fairly frequent in the upper elevations of the Sierra San Pedro Mártir. The new species is tentatively considered to be related to *P. strictiramea,* and to be near to *P.* sect. *Homalopoa* Dumort.

Resumen

Se discribe una nueva graminea perenne, *Poa bajaensis,* de Baja California, Mexico. Se compara con *P. strictiramea* Hitchc. y el tipo de *P. orcuttiana* Vasey. Este especies, por mucha tiempo se denominó *P. orcuttiana* en los herbarios. Se puede distinguir de las otras dos, por las cortas hojas de caulinares de la parte superior, por las vainas mas cercanas, y por las hojas abaxialmente mas lisas y las ramas de paniculas mas lisas. Es aparentemente endemica, y mas o menos frequente en las elevacíones superiores de da Sierra San Pedro Mártir. La nueva especie tentativemente esta relacionada con *P. strictiramea,* y parece estar cercana a *P.* sect. *Homalpoa* Dumort.

A new and distinctive species of *Poa* is here named after the Baja California Peninsula of Mexico. The new species is known only from the upper elevations of the Sierra San Pedro Mártir. It has been collected there in the spring on several occasions, and seems to be fairly frequent. Specimens included here were treated as *P. orcuttiana* Vasey by Gould and Moran (1981), and have since passed under that name. So far as I am aware, J. D. Olmsted, in 1962, was the first person to collect the new species. I realized it was probably new when I first examined a specimen of it while working on my dissertation at New Mexico State University in the early 1980s, but needed to see more material and to compare it with the type specimen of *P. orcuttiana.*

Poa bajaensis Soreng, sp. nov. (Fig. 1)—TYPE: Mexico, Baja California, Sierra San Pedro Mártir, east rim above Yerba Buena, 31°01′N, 115°26′W, elev. 2700 m, common in duff under trees, 1 Jun 1968, *Reid Moran 15070* (Holotype, US-259736; isotype: SD-69304).

A *Poa strictiramea* similis sed in paniculis 4–13 cm longis (versus 10–30 cm) foliorum vaginis nodorum superiorum connatis 29–36% (versus 10% vel minor) laminis nodorum superiorum abbreviatis, 0.1–1.5(4) cm longis multo brevioribus quam vaginis (versus plerumque longioribus) laminis abaxialiter laevibus (versus plerumque scabris) differt.

Perennial, densely tufted, without rhizomes. Basal tuft of leaves 5–10(15) cm tall. Basal sheaths often persisting into the next growth season, papery (not anastomosing). New vegetative shoots emerging intravaginally; prophylls 1–2 cm long, split abaxially, scabrous and pilose on the 2 keels. *Culms* 20–50 cm tall, top 1–2 leaf nodes well exposed or barely enclosed, all lower nodes enclosed in their sheaths. *Leaves:* sheaths slightly keeled, very sparsely to moderately (rarely densely), evenly, finely scabrous, uppermost culm sheaths 8–15 cm, margins fused 29–36% of the length; collars not noticeably more scabrous than their sheaths; ligules of vegetative and lower culm leaves membranous, 0.25–0.5 mm, of upper culm leaves 0.5–1.5(2) mm, apex truncate to obtuse, backs and apical margins densely scabrous; culm and vegetative leaf-blades similar, flat or folded, moderately thick, with involute margins, abaxially smooth or very sparsely and finely scabrous, to moderately scabrous apically, veins weakly expressed adaxially and abaxially, adaxially smooth or moderately to densely finely scabrous, longest blades less than 5 cm, uppermost culm blade 0.1–1.5(4) cm, blades 1.5–2.75 mm wide (expanded), narrowly and abruptly prow-tipped. *Panicles* 4–13 cm, not or slightly to highly anthocyanic, erect, open, sparse, lower axis smooth, lowest internodes 1.8–3.9(5.2) cm; branches 2–3(5) per lower node, widely spreading to reflexed, fairly strict, smooth or very sparsely finely scabrous proximally, smooth or moderately (rarely densely) finely scabrous distally, terete or weakly angled, hooks not confined to rows on angles, the longest branches 3–7 cm, with 5–15 spikelets. *Spikelets* 3.75–8 mm; glumes and lemmas distinctly keeled, glumes thin, smooth or sparsely scabrous on the upper keel
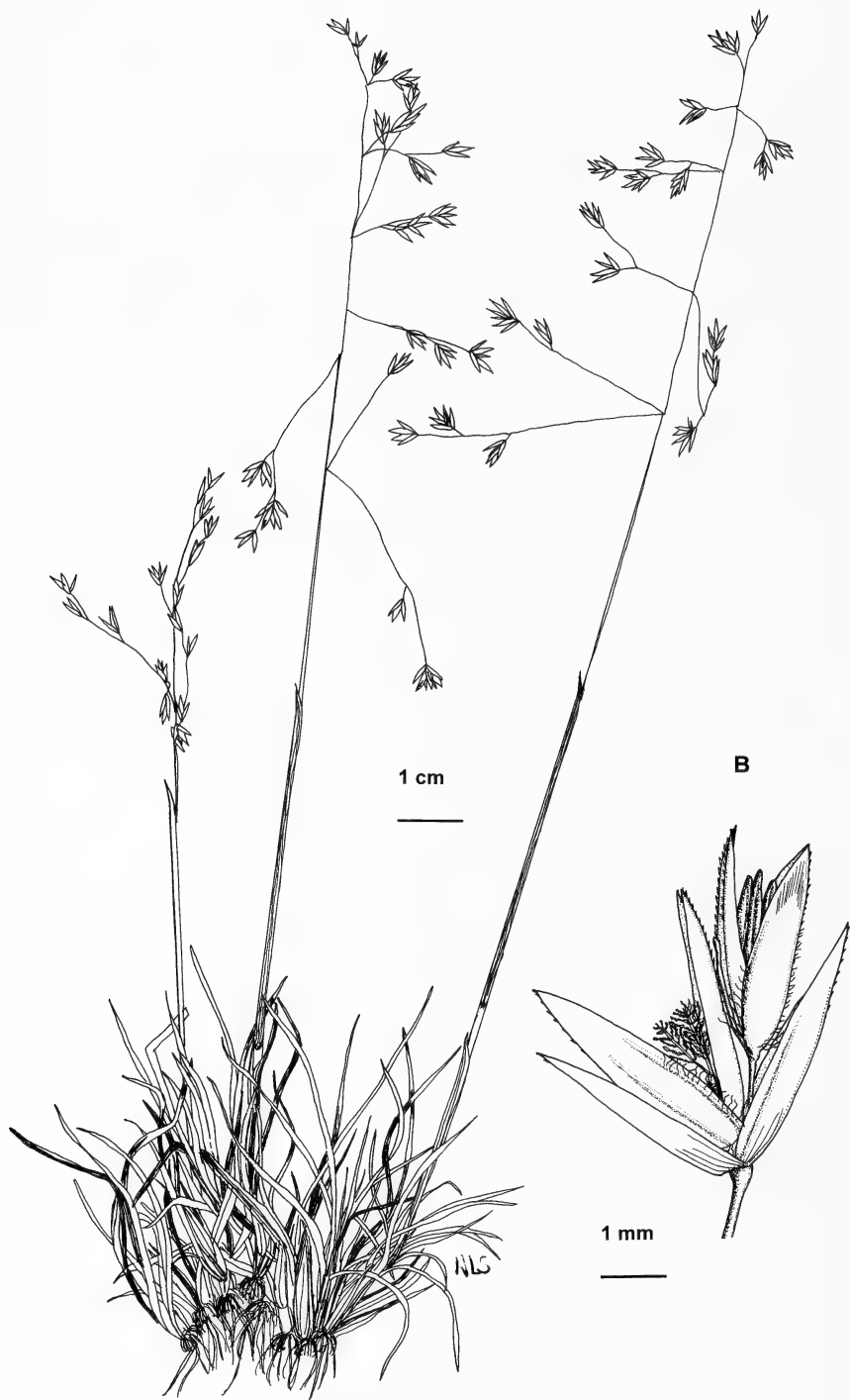
Fig. 1. *Poa bajaensis* Soreng, illustrated from the holotype collection, *Reid Moran 15070* (US-259736). A. Habit. B. Spikelet.

and sometimes on the lateral veins, and sometimes between them, ½ to ¾ the length of adjacent lemmas, the first 2.5–3 mm, 1(–3)veined, the second 2.8–3.5 mm, 3-veined, more than two times as wide as the first; rachillas smooth, longest internodes 1.25–2 mm; florets (1)2–4(6); calluses of some plants all glabrous, of other plants infrequently to frequently with 1–several woolly dorsal hairs up to 2 mm long; lemmas 3.2–4.2 mm, 5-veined, distinctly keeled, apically sparsely scabrous on the

keel, lateral veins weakly expressed, the body and other veins smooth, entirely glabrous in one plant, or softly puberulent, hairs to 0.5 mm on the keel and marginal veins, to 0.2 mm on the sides between the veins and sparsely to densely covering the lower ½–⅘, apex acute, entire; palea approximately equaling the lemma in length, keels nearly smooth to closely and finely scabrous, glabrous or sparsely puberulent near the middle on and between the keels. *Flowers* perfect; anthers 1.7–3.2 mm (rarely sterile, but then ca. 1.7–1.8 mm).

Paratypes. Mexico, Baja California [Norte]: Sierra San Pedro Mártir: Crest of range N of observatory, head of Cañada el Copal and S slope of Cero Venado Blanco, 2500–2700 m, 3 Jun 1988, *S. Boyd, T. Ross, K. McCulloh 2311* (RSA); La Concepcíon, 31°01′N–115°37′W, ca. 1450 m, 31 May 1968, *Reid Moran 15006* (SD); open W slope of Cerro 2828, ca. 31°02′N–115°27′W, ca. 2800 m, 31 May 1968, *Reid Moran 15060* (BH, SD); 2 mi W of Vallecitos, 31°00′N–115°29′W, ca. 2250 m, 2 Jun 1968, *Reid Moran 15083* (SD); 3 km NE of El Alto de Corona, 31°00′N–115°41′W, ca. 2400 m, 20 Aug 1977, *Reid Moran 24555* (SD); W slope below summit of El Picacho, 30°59′30″N–115°22′30″W, ca. 2950 m, 5 May 1978, *Reid Moran 25611* (SD); end of road into high end of northern sierra, ca. 64 mi. from end of paved road to Ensenada, 7200 ft (2210 m), 6 Jun 1962, *J. D. Olmsted 4561* (RSA; somewhat intermediate to *P. secunda*); Central [region], ca. 3 mi. ESE of Prado del Corona, ca. 1 mi. up canyon from southernmost aspen colony, tributary of Rio San Rafael, 8100 ft (2490 m), 9 Jun 1962, *J. D. Olmsted 4711* (RSA); S of Vallecitos near Cerro la Botella Azul, 30°57′20″N–115°25′26″W, ca 2440 m, 27 Jun 1998, *J. Rebman & A. Russell 5384* (US); near crest of mountain range, approx. 2 mi SE of the observatory, 31°14′N–115°64′W, ca. 2985 m, 28 Jun 1998, *J. Rebman & A. Russell 5384* (SD); "Corral Meadow", 7.5 km NW (340°) of the observatory, 31°06′45″N–115°29′50″W, 16 Jun 1988, *A. C. Sanders, R. Minnich, E. Franco M. Salazar 7895* (RSA, SD); Vallecitos, ca. 31°02′N–115°28′W, ca. 2430 m, 18 Jun 1985, *R. F. Thorne, R. Dahlgren, S. Boyd & D. Charlton 60858* (RSA, SD); Vallecitos, ca. 31°02′N–115°27.5′W, ca. 2430 m, 1 Sep 1985, *R. F. Thorne, M. Z. Thorne, L. Thorne & T. Petrella 61394* (RSA); just above observatory living quarters, ca. 31°02′N–115°28′W, ca. 2600 m, 7 May 1986, *R. F. Thorne, T. S. Elias & Paulino Rojas 61967* (MO-3333160, RSA); near gate to UNAM Observatory, 31°02′N–115°29′30″W, 2520 m, 29 May 1982, *G. Yatskievych, S. Forbes, M. Gallagher, J. Evans & A. Kelley 82-190* (SD).

Habitat characteristics. Mountain slopes, flats and drainages, in Salix and Populus tremuloides thickets, *Quercus-Pinus jeffreyi* forests, and *Quercus-P. jeffreyi-P. lambertiana-Abies concolor* forests, and open meadows of *Pinus jeffreyi* park, in sandy to rocky to clayey, sometimes duff-covered, granitic soils, 1450–2950 m elev. Flowering May to June.

Discussion. Herbarium specimens of the new species had been determined as: *P. fendleriana* (Steud.) Vasey (*P.* sect. *Madropoa* Marsh ex Soreng); *P. interior* Rydb. (*P.* sect. *Stenopoa* Dumort.); or most commonly as *P. orcuttiana* Vasey (=*P. secunda* J. Presl subsp. *secunda; P.* sect. *Secundae* Marsh ex Soreng). Although it seems to have little in common with any of these taxa, it is superficially similar in a few respects to the type of *P. orcuttiana.*

Poa orcuttiana was placed in synonymy under *P. scabrella* Vasey by Hitchcock (1951) and Keck (1959), and (along with *P. scabrella*) in *P. secunda* J. Presl by Kellogg (1986). The type of *P. orcuttiana* is typical of material that has been recognized as *P. scabrella* (Hitchcock 1951; Keck 1959; Gould and Moran 1981). It fits well within the range of morphological variation found in *P. secunda* subsp. *secunda* in which *P. scabrella* is included by Soreng (1994; *P. orcuttiana* was considered a minor synonym of *P. scabrella sensu* Hitchcock or Keck, and thus was not included in the brief synonymy published there). However, Gould and Moran (1981) recognized both *P. scabrella* and *P. orcuttiana* in their treatment of grasses of Baja California, Mexico. Gould and Moran's description of *P. orcuttiana,* its habitat, range (except for the stated range in southern California), and key, match the new species perfectly. To clear up this contradiction it is necessary to compare the type of *P. orcuttiana* with the new species in detail.

The type specimen of *P. orcuttiana* Vasey (Holotype: USA, California, San Diego, Chollas [a site below 150 m elevation], 26 May 1884, *C. R. Orcutt 1070* (US-556833), West. Amer. Scientist 3: 165. 1887.), has long, narrow (0.5 mm), very thin, and sparsely to moderately densely and coarsely scabrous blades, the basal tuft 20 cm tall, upper culm blades 4.5–7 cm long (⅖ to ½ the length of their sheaths), with acute or lacerate ligules 2.75–3.25 mm long. The sheaths are open to near the base and are moderately densely, coarsely scabrous. The panicles are contracted, or, on one culm in anthesis (probably lending to past confusion with the new species), open with somewhat spreading branches. (It is usual for *P. secunda* panicles to open up at anthesis and later contract, though they remain open in some ecotypes of sheltered habitats.) The panicle branches are densely and coarsely scabrous throughout. The spikelets have 5–8 florets, with sparsely scabrous rachillas, first glumes with 3 veins, calluses glabrous or with a short crown of hairs surrounding the lemma base, and lemmas rounded on the back and quite scabrous, with short sparse pubescence mainly on the keel and marginal veins.

The new species differs in several respects from

TABLE 1. COMPARISON OF *POA BAJAENSIS* WITH *P. STRICTIRAMEA* AND THE TYPE OF *P. ORCUTTIANA*. Character states typical of the *P. scabrella* form of *P. secunda* subsp. *secunda* are indicated by *.

Characters	Species *P. bajaensis*	Type specimen *P. orcuttiana*	Species *P. strictiramea*
Culm length	20–50 cm	60–70 cm*	30–90 cm
Blade shape and thickness	flat or folded with involute margins, moderately thick	flat*, thin*	flat or folded with involute margins, moderately thick
Blade abaxial scabrosity	smooth or very sparse throughout to moderate apically, fine	sparse to moderately-dense*, coarse*	sparse to dense, coarse
Basal leaf tuft height	5–10 (–15) cm	20 cm*	15–30 cm
Leaf blade and sheath persistence	persisting	soon withering*	persisting
Top leaf blade length	0.1–1.5 (–4) cm	4.5–7 cm*	7–15 cm [complete data unavailable]
Top blade-to-sheath length ratio	< 1:5 (rarely more)	2:5–1:2*	mostly > 1:1
Top ligule length	0.5–1.5 (–2) mm	2.75–3.25 mm*	0.5–4 (–6) mm
Top ligule apex	truncate to obtuse	acute or lacerate*	truncate to acute
Sheath closure from base	29–36%	closed only near the base or up to 10%*	closed only near the base or up to 10%
Panicle length, shape, and branch angle of divergence	4–13 cm, open, branches widely spreading to reflexed	14 cm*, contracted*, branches ascending, or during anthesis open with branches somewhat spreading*	(7–) 10–30 cm, open, branches spreading
Panicle branch scabrosity	smooth or sparse proximally, smooth or moderate to dense distally, fine	dense* and coarse* throughout*	moderate to dense on the angles throughout, fine to coarse
Spikelet no. of florets	(1–) 2–4 (–6)	5–8*	2–5
Rachilla vesture	smooth, glabrous	sparsely scabrous*, glabrous	smooth or scabrous, sometimes sparsely hirtellous
First glume no. of veins	1 (–3 faint)	3*	1–3
Callus pubescence	glabrous, or with a sparse dorsal web	glabrous, or with a crown of short hairs*	glabrous, rarely with a sparse dorsal web
Lemma shape	keeled	rounded on back*	keeled
Lemma scabrosity	smooth	distinctly scabrous*	smooth or sparsely to densely scabrous

the type of *P. orcuttiana* (Table 1). The scabrosity of the leaves is much finer, and sparse or absent on the abaxial surface and denser on the adaxial surface; the sheaths are closed over a greater portion of their length; the leaf-blades are shorter (the upper culm blades mostly less than 1/5 the length of their sheaths), broader, thicker, firmer, and flat or more often folded; and the ligules are shorter and truncate. The inflorescence remains open and the branches are widely spreading to reflexed and are smooth or only sparsely scabrous distally (moderately scabrous in **Olmsted 4561,** which also has a 4-cm-long upper blade [2/5 the sheath in length], sterile anthers, and is perhaps intermediate between *P. bajaensis* and *P. secunda*). The spikelets usually have fewer (2–4) florets; the first glumes are mostly 1-veined; the rachillas are smooth; the lemmas are keeled; and the calluses sometimes have a dorsal web (never a crown of hairs).

Poa scabrella, as treated by Keck (1959) and by Gould and Moran (1981), is said to occur mainly below 1500 m, and is not known to reach into higher elevations of the Sierra San Pedro Mártir. The new species occurs mainly above 2200 m.

The degree of closure of the sheaths, the smoothness of the branches, and the presence of 1-veined first glumes exclude this species from *P.* sect. *Stenopoa.* In addition, the keeled spikelets and lemmas and the occurrence of a dorsally isolated web on the callus exclude this species from *P.* sect. *Secundae.* There is no evidence of dicliny in *P. bajaensis,* eliminating the possibility it belongs to *P.* sect. *Madropoa, P.* sect. *Dioicopoa* E. Desv., or the *P. nervosa* complex of *P.* sect. *Homalopoa* Dumort., all of which exhibit pistillate flowers (with rudimentary anthers) in many plants (Soreng 2000).

The new species is most similar to *Poa strictiramea* Hitchc. (Table 1; syn. *P. involuta* Hitchc.) of the mountains in and around the Chihuahuan Desert and the eastern Sierra Madre Occidental. The nearest site I am aware of for the latter species is in northwest Chihuahua, near Babicora, over 850 km ESE. The new species is tentatively considered to be allied to *P. strictiramea* and its rhizomatous relative *P. ruprechtii* Peyr. of the Sierra Madre Oriental. It is placed *incertae sedis,* near to the latter two species, these near to *P.* sect. *Homalopoa* Dumort.

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REVIEW

Trees and Shrubs of California, by John D. Stuart and John O. Sawyer. Illustrated by Andrea J. Pickart. 2001. 467 pp. University of California Press, Berkeley. Hardcover $45.00 ISBN 0-520-22109-5, softcover $22.50 ISBN 0-520-22110-9.

So far, being seriously interested in woody taxa in California meant carrying a subset of the below listed publications plus The Jepson Manual to the field. Will this new guide to trees and shrubs of California replace all that? Yes, to some extent. This will be a useful book for beginners. Almost all native California trees are here and many common shrubs. Some commonly naturalized woody species are here as well. Keys are friendly, based on readily available vegetative characters. Reproductive structures are needed only exceptionally. Technical terms are kept to minimum; all of them are explained in the glossary. Nomenclature follows The Jepson Manual, with some justifiable exceptions (e.g., rehabilitation of the genus *Chamaecyparis*). About ⅔ of the included species are illustrated by line drawings. Unfortunately, some, like those of *Cercis occidentalis, Genista monspessulana,* or *Salix gooddingii,* are of rather marginal quality to say the least. Thirty nine color photographs are, in general, excellent. The distribution of 313 species in California is illustrated by small range maps. For many of the species, these are the first sketches of distributional maps ever completed. Some more or less relevant references are listed; several really useful ones are missing (e.g., Benson and Darrow 1981; McMinn and Maino 1980; Petrides and Petrides 1992; Sampson and Jespersen 1981; Sudworth 1967).

I do not expect any complaints about coverage of California trees. Only very rare species like *Lyonothamnus floribundus* are missing. However, if you do not know some less common shrubs, like *Forestiera pubescens, Fouquieria splendens, Lotus scoparius, Peraphyllum ramosissimum, Ribes malvaceum,* or *Romneya coulteri,* you will be lost. They are not included. Some genera with common woody species like *Amorpha, Brickellia* or *Penstemon* are not treated at all. Nevertheless, *Neviusia cliftonii* is here. If you collect one of the more than 40 excluded species of *Arctostaphylos,* you should retreat to The Jepson Manual or, even better, to Wells' (2000) book on manzanitas. If it happens that you find *Quercus palmeri,* or *Q. tomenlella,* you will certainly be more successful with Pavlik et al. (1991) or Roberts' (1995) manuals. Stuart and Sawyer's guide, as the authors themselves admit, is clearly less useful in southern California where other sources will have to be consulted (e.g., Benson

and Darrow 1981; Conrad 1987; Elmore and Janish 1976). Several invasive woody species, even if currently not really widespread in California, could be included in a manual like this (e.g., *Acacia dealbata, Alhagi pseudalhagi, Catalpa bignonioides, Cotoneaster* spp., *Crataegus monogyna, Elaeagnus angustifolia, Fraxinus uhdei, Ligustrum* spp., *Myoporum laetum, Nicotiana glauca, Sapium sebiferum, Schinus molle, Sesbania punicea*). Their early detection can be critical for their successful control or eradication.

There are regions, like Great Britain, south-eastern Australia, New Zealand, or Kenya with a long tradition of excellent complete (or almost complete) field guides to trees and shrubs. Recently published Brayshaw's (1996) guide to woody species of British Columbia also belongs in this category. Stuart and Sawyer's guide is just a first step in the right direction.

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PHYSIOLOGICAL AND ANATOMICAL ASPECTS OF CAM-CYCLING IN *LEWISIA COTYLEDON* VAR. *COTYLEDON* (PORTULACACEAE)

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ABSTRACT

We investigated leaf morphology, CO_2 uptake, and the diurnal acid fluctuation of the montane species, *Lewisia cotyledon* Robinson. This species belongs to the Portulacaceae, a small family with ~ 425 species, which exhibit photosynthetic flexibility. *Lewisia cotyledon* was found in the Siskiyou Mts. in Josephine County, OR along with other montane species that utilize the CAM pathway. Plants were collected and returned to the greenhouse to study the photosynthetic metabolism of this species under both well-watered and drought conditions. *Lewisia cotyledon* showed primarily daytime CO_2 gas exchange. Well-watered plants exhibited a significant diurnal acid fluctuation during the day. Phosphoenolpyruvate (PEP) carboxylase (EC 4.1.1.31) activity was low in both control and water-stressed plants. Leaf anatomy showed a CAM-like spongy mesophyll tissue with palisade mesophyll tissue atypical of C_3 plants. The percentage of leaf air space was 16.8%, which is characteristic of CAM and CAM-cycling plants. Water stress did not induce CAM metabolism. Our results suggest that: 1) *L. cotyledon* exhibited the CAM cycling pathway that would better enable the plant to withstand water stress and high light environments; 2) CAM is more widespread in the Portulacaceae than was previously thought; and 3) the evolution of the CAM pathway in the Portulacaceae appears to require the acquisition of both physiological and anatomical modifications.

Crassulacean acid metabolism (CAM) is a photosynthetic pathway that is characterized by net nighttime carbon dioxide (CO_2) uptake (Kluge and Ting 1978; Ting 1985; Winter and Smith 1995). The CO_2 is stored as malic acid in the plant's central vacuole during the night period. The malate is then decarboxylated to release CO_2 to be used in the PCR (photosynthetic carbon reduction) cycle in the subsequent light period. During the day, due to high CO_2, CAM plants close their stomata to maintain high internal CO_2 levels for photosynthesis. The closure of the stomata subsequently reduces the amount of water loss due to transpiration. Thus, these plants are usually found in environments where water availability becomes restricted temporarily or seasonally, such as in deserts or rock outcrops, or as in epiphytes. There are two criteria for easily distinguishing CAM plants from C_3 plants which exhibit daytime CO_2 uptake; one criterion is nocturnal CO_2 uptake, and the other is a diurnal acid fluctuation where organic acid levels are high in the morning and low in the evening.

Variations of CAM have been shown in many other plants. One modification is called CAM-cycling (Ting 1985). In CAM-cycling, plants do not completely shut their stomata during the day and fix little or no exogenous CO_2 during the night. Plants still use malic acid to store CO_2 but it comes primarily from recycling of CO_2 from respiration at night (Ting 1985). CAM-cycling has been noted in many plants, for example, *Talinum* spp. (Martin and Zee 1983; Martin et al. 1988a), *Peperomia* spp.

(Sipes and Ting 1985) and *Portulacaria afra* (L.) Jacq. (Guralnick et al. 1992).

Another variation of CAM is called CAM-idling. CAM-idling plants close their stomata day and night in response to low water availability but still show slight diurnal acid fluctuations. It is hypothesized that these plants maintain low levels of metabolic activity and can respond quickly to rainfall when the opportunity arises (Ting 1985). CAM-idling has been described in many plants, for example, *Opuntia basilaris* Engelm. & Bigelow (Szarek and Ting 1974), *Xerosicycos danguyii* H. Humb. (Rayder and Ting 1983), and *P. afra* (Guralnick and Ting 1987).

Lewisia cotyledon is a small plant with thick fleshy leaves. *Lewisia* belongs to the small but widely distributed family Portulacaceae. The western North America taxa of Portulacaceae (*Lewisia, Claytonia, Calyptridium,* and *Montia*) have been considered to be primarily C_3 plants (Nyananyo 1985). In a phylogenetic study, the western North America taxa were grouped together taxonomically as C_3 plants (Hershkovitz and Zimmer 1997). We have studied the photosynthetic pathways of many genera in this family, including *Montia, Portulacaria, Talinopsis, Portulaca, Anacampseros, Calandrinia, Talinum,* and *Calyptridium* (Guralnick and Jackson 2001). The photosynthetic diversity of the Portulacaceae is considerable despite the small size of the family. Some are considered typical C_3 plants (Nyananyo 1985). Other members show CAM-cycling (Martin et al. 1988a, b) while others are C_4 plants and also show CAM-cycling (Koch and Kennedy 1980, 1982; Kraybill and Martin 1996). Still other members of the family are suc-

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culent species that are facultative CAM plants and shift between C_3 and CAM depending on environmental conditions (Ting and Hanscom 1977; Guralnick et al. 1984; Guralnick and Ting 1988).

Lewisia cotyledon is a montane species suspected of being CAM. *Lewisia* is considered to be drought-tolerant, occurring in rocky outcrops or on gravelly ridges that do not retain water well (Hohn 1975). This montane species undergoes significant water stress during the course of the summer due to the lack of rainfall during the months of May through September (Hohn 1975). The species grows in close association with *Sedum* spp. in which photosynthetic pathway flexibility is better known. Based on these observations the investigators hypothesize that this montane species may possess metabolic or structural adaptations typical of CAM plants. This would enable *Lewisia* to withstand the typical summer droughts of the Siskiyou Mountains.

The objectives of this study were to determine the type of photosynthetic pathway utilized by *Lewisia* since the photosynthetic flexibility of the genus has not been studied. This project was designed to determine what, if any, attributes of the CAM pathway *Lewisia* exhibited. This current study has indicated that attributes of the CAM-cycling pathway are more widespread in the Portulacaceae than was previously reported.

Materials and Methods

Plant material. Plants of *L.c.* var. *cotyledon* were collected from the Siskiyou Mountains in Josephine Co. of southern Oregon and transplanted into 2-L pots in a glasshouse on the campus of Western Oregon University. Additional plants were purchased from the Rare Plant Research Institute (Portland, OR). All plants were irrigated prior to the studies with 1/2-strength Hoagland's solution. The plants were grown under natural light conditions with a light intensity of 600 μmol m^{-2} s^{-1} during the summer months. During the winter months, the plants were grown with a 14-hour light/10-hour dark cycle with diffuse sunlight of 200 μmol m^{-2} s^{-1} supplemented with artificial light of 400 μmol m^{-2} s^{-1}. To study potential shifts in photosynthetic metabolism, water was withheld from the plants for up to 10 days. Experiments were repeated four separate times with typical results of one experiment reported.

Titratable acidity. Four leaves were collected in the morning and evening and were frozen ($-20°C$) until assayed a week later. Leaf punches of ca. 0.8 cm^2 were taken with a cork borer and weighed. The punches were ground in glass distilled water and titrated with 0.01 N-KOH to a pH 7 endpoint.

CO_2 uptake. CO_2 uptake was measured using a CID-301 PS portable photosynthesis system (CID, Inc., Vancouver, WA). Four to six intact leaves were measured per timepoint over a 24-hr cycle in a typical experiment.

PEP carboxylase activity. Leaf samples for PEP-Case activity were collected in triplicate in the late afternoon when inhibition from malate would be the lowest. Approximately 1 g of tissue was collected for each sample and ground in 10 ml of 100 mM Hepes-KOH, 10 mM MgCl$_2$, 10 mM DTT, 1% (w/v) polyvinlypyrolidone, and 1% (v/v) Triton X-100 adjusted to pH 7.8. An aliquot of 1 ml was taken for chlorophyll determination as described by Guralnick and Ting (1988). The sample was centrifuged at 10,000 rpm for 15 min at 4°C. The crude extract was used to assay enzyme activity spectrophotometrically by following the oxidation of NADH at 340 nm. The assay mixture contained 100 mM Hepes-KOH (pH 7.8), 10 mM MgCl$_2$, 1 mM NaHCO$_3$, 0.2 mM NADH, 3 mM PEP, and 200 μl crude extract in a total volume of 3 ml.

Mesophyll succulence. Mesophyll succulence (S_m) was calculated from the ratio of total tissue water to total chlorophyll in fresh leaf samples (Kluge and Ting 1978). Tissue water content was determined by drying samples in an oven and subtracting the dry weight from the fresh weight. Chlorophyll was determined by grinding fresh leaf tissue in 5 ml of 80% acetone and then centrifuging the sample at 2500 rpm. A 3 ml aliquot was taken and measured spectrophotometrically (Guralnick et al. 1986).

Leaf anatomy. Mature leaves were collected and fixed in 2% paraformaldehyde and 1.25% glutaraldehyde in 50 mM PIPES at pH 7.2 for 24 hr. at 4°C. The tissue was sequentially dehydrated in an ethanol series, infiltrated with LR White acrylic resin, and 1 μm sections were placed on gelatin-coated slides. Sections were stained with Stevenel's blue for 1 min, and then with 0.5% safranin O for 30 sec. Stereological methods were used to quantify the percentage of mesophyll airspace in five different leaves according to Guralnick et al. (1986).

Results

CO_2 uptake. Irrigated plants of *Lewisia* were found to have primarily daytime CO_2 uptake with no nighttime CO_2 uptake (Fig. 1) though some leaves of *Lewisia* did show a positive nocturnal CO_2 uptake. When water was withheld from *Lewisia* for three days, daytime CO_2 uptake was reduced and there was no concomitant increase in nighttime CO_2 uptake (Fig. 1). Withholding water for seven days did not increase the nighttime CO_2 uptake (Fig. 1). Plants that were stressed for 10 days also showed reduced day and night CO_2 uptake, which was indicative of CAM-idling (data not shown). Nocturnal release of respiratory CO_2 was usually greater but not different during the night in irrigated plants compared to water-stressed plants for all treatments (Fig. 1).

Titratable acidity. A slight diurnal acid fluctuation of 20 μeq g^{-1} FW was observed in control
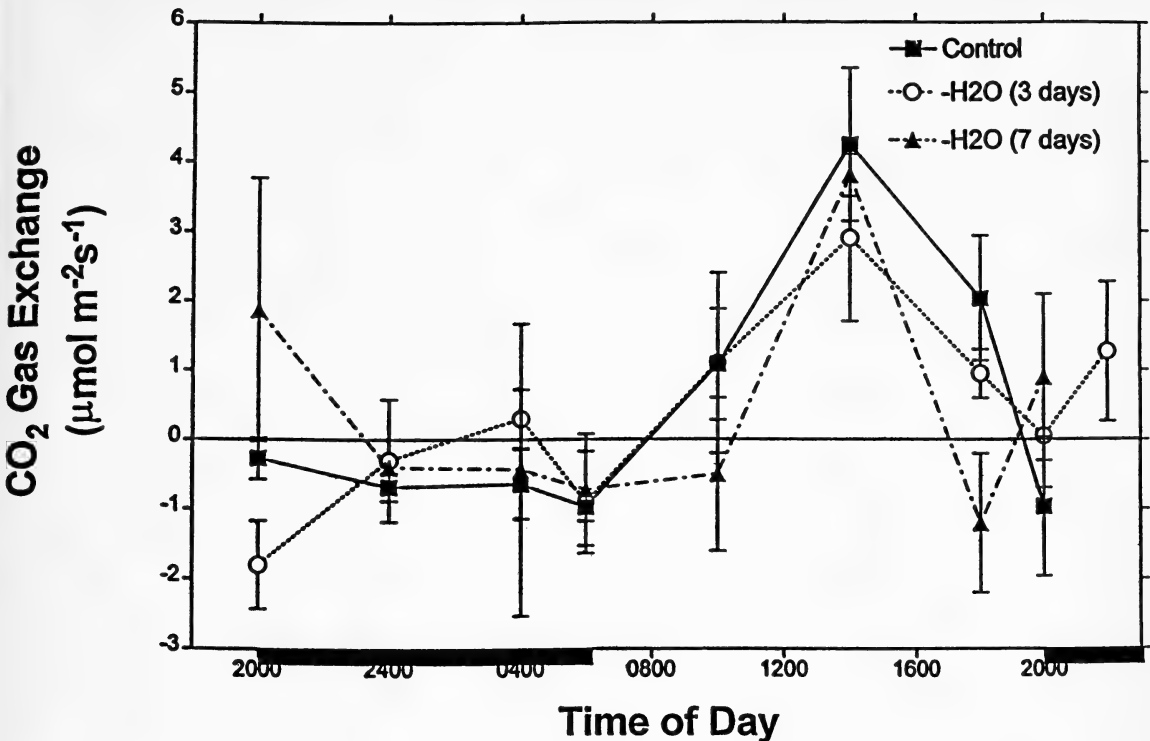
Fig. 1.   Diurnal variation in CO_2 gas exchange in control and water-stressed plants for three and seven days in *Lewisia cotyledon.* Black bar indicates the night period and error bars represent 1 SE for all figures. Typical results of one experiment are shown.

plants with morning acid levels significantly different than afternoon acid levels (Fig. 2, t-test, P < 0.05, n = 4). Water stress for 10 days dampened the day/nighttime differences in acidification relative to the control plants (Fig. 2). Morning and evening acid levels were not significantly different in 10-day water-stressed plants (Fig. 2, t-test, P > 0.05, n = 4). Plants stressed for seven days showed reduced morning and evening acid levels with sig-

nificant diurnal acid fluctuation half as large when compared to control plants (Fig. 2).

PEP carboxylase activity. PEPCase activity in control plants was 1.75 μmol mg chl^{-1} min^{-1} throughout the experimental period. PEPCase activity in the water-stressed plants was 2.00 μmol mg chl^{-1} min^{-1} and did not show any increase after ten days of water stress. The activity of the water stress plants was not statistically significant from the control PEPCase activity levels.

Leaf anatomy and mesophyll succulence. Mesophyll succulence was 6.33 g H_2O mg chl^{-1} and in the range of other CAM and CAM-cycling plants (Fig. 3). *Lewisia* leaves did not have the typical C_3 appearance in which the mesophyll was well organized and differentiated into palisade and spongy mesophyll tissue (Figs. 4, 5). A very prominent spongy mesophyll was observed which was typical of CAM plants. The palisade parenchyma layer showed some organization but was not organized into rows of cells. The palisade cells were elongated and rounded at the ends. The palisade cells also contained a very large central vacuole (Figs. 4, 5). The percentage of airspace in the mesophyll tissue was 16.8 $\pm$ 4.5% (Table 1).
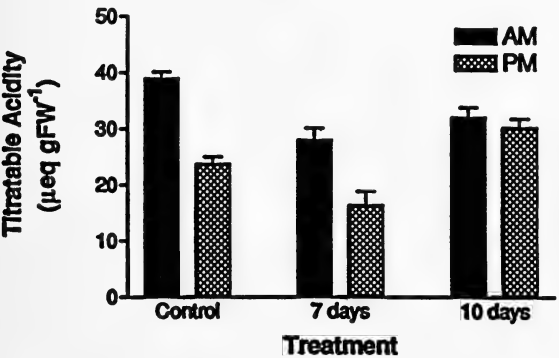

Fig. 2.   Diurnal fluctuation of total titratable acids. Samples were taken at sunrise and sunset. Control and 7 day water-stressed plants showed a significantly higher a.m. acid levels than p.m. acid levels (P < 0.01, n = 4).
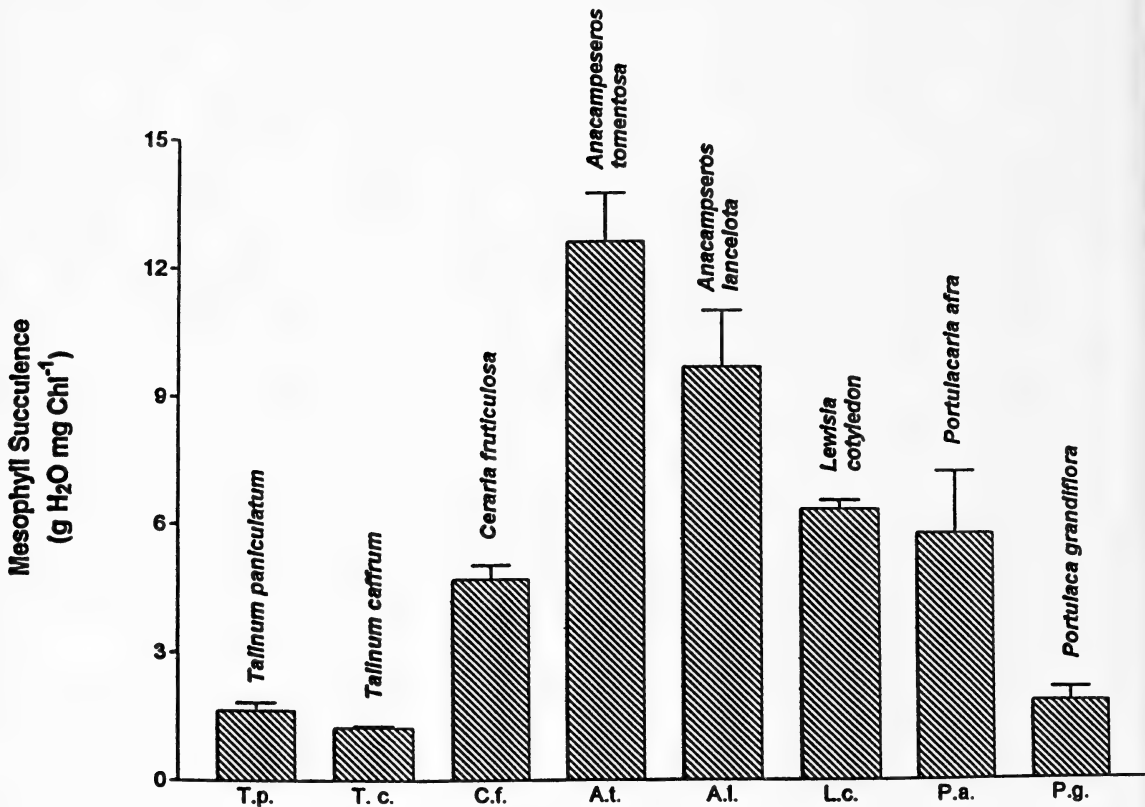
Fig. 3.   Mesophyll succulence (S_M) of whole leaves for selected genera of the Portulacaceae.

Discussion

In a study of the Portulacaceae, *Lewisia cotyledon* was described as a C_3 plant (Nyananyo 1985). In addition, Hershkovitz and Zimmer (1997) in their phylogenetic analysis of the Portulacaceae, indicated that *Lewisia* fell into the C_3 group of North American taxa. Our results indicate that *Lewisia* shows aspects of CAM-cycling. Well-watered plants showed gas exchange patterns typical of C_3 photosynthesis: exogenous CO_2 uptake during the day and little, if any, nocturnal CO_2 uptake. *Lewisia* had higher titratable acid levels and a small but significant diurnal acid fluctuation not observed in typical C_3 plants and indicates CAM-cycling (Kluge and Ting 1978; Ting 1985; Guralnick et al. 1992;). The acid fluctuation was similar in magnitude to other CAM-cycling species (Martin and Zee 1983; Harris and Martin 1991a; Guralnick et al. 1992).

The physiological data did not support the hypothesis that *L. cotyledon* was a facultative CAM species. Well-watered plants showed no nocturnal CO_2 uptake and low PEPCase activity when compared to other CAM species such as *Portulacaria* (Guralnick and Jackson 2001). Drought did not induce CAM in this species even after withholding water for up to 10 days whereas 10 days of drought in *Talinum triangulare* produced a slight increase

in nocturnal CO_2 uptake and an increase in PEPCase activity (Herrera et al. 1991).

Nocturnal CO_2 output in irrigated *Lewisia* was comparable to other CAM-cycling species such as *Talinum* (Martin and Zee 1983; Harris and Martin 1991b), *Peperomia* (Sipes and Ting 1985), *Sedum* (Martin et al. 1988a), and *Portulaca* (Kraybill and Martin 1996). There was also a comparable increase in titratable acids that we attribute to a recycling of respiratory CO_2 (Ting 1985). This widespread occurrence of CAM-cycling appears to have some adaptive significance. Martin and Zee (1983) and Martin et al. (1988b) have calculated that CAM-cycling species could show a significant reduction in water loss through decreased transpiration because of the endogenous source of CO_2. Another consequence of CAM-cycling is that the accumulation of malic acid in the vacuole may aid in osmotic water uptake (Eller and Reuss 1984, 1986). These adaptations may contribute to the survival of *Lewisia* in highly exposed areas such as rock outcrops, where water availability is reduced for prolonged periods.

The leaf structure of *Lewisia* was found to be typical in some aspects to other CAM and CAM-cycling species. Leaves of CAM plants are characterized by tightly packed chlorenchyma with large vacuoles where the malic acid accumulates
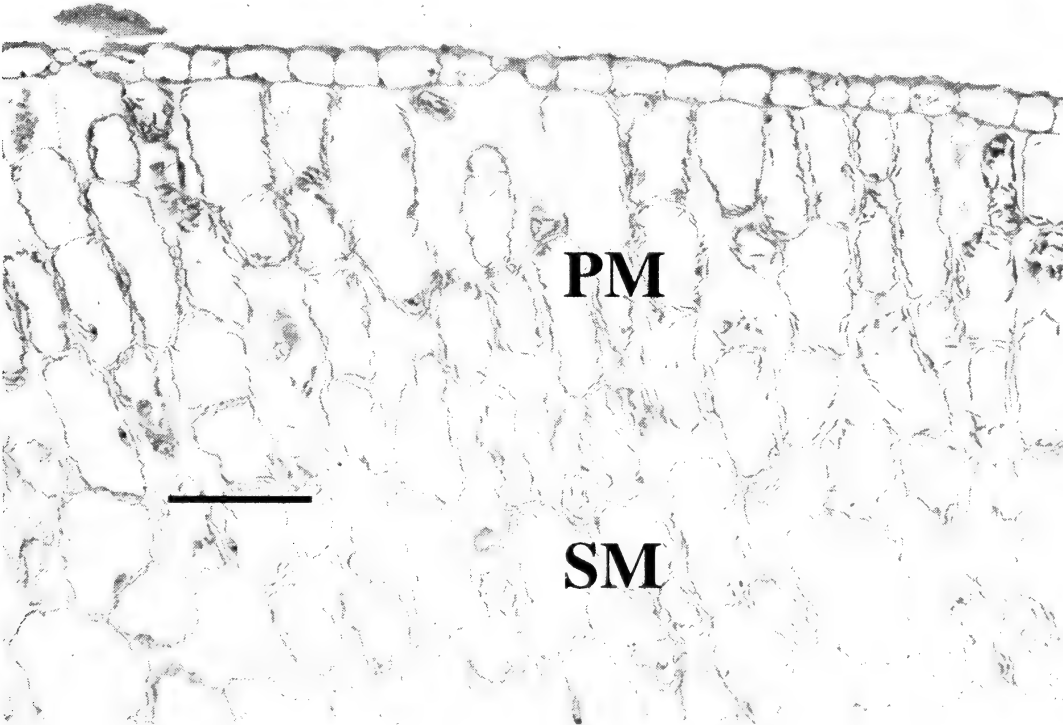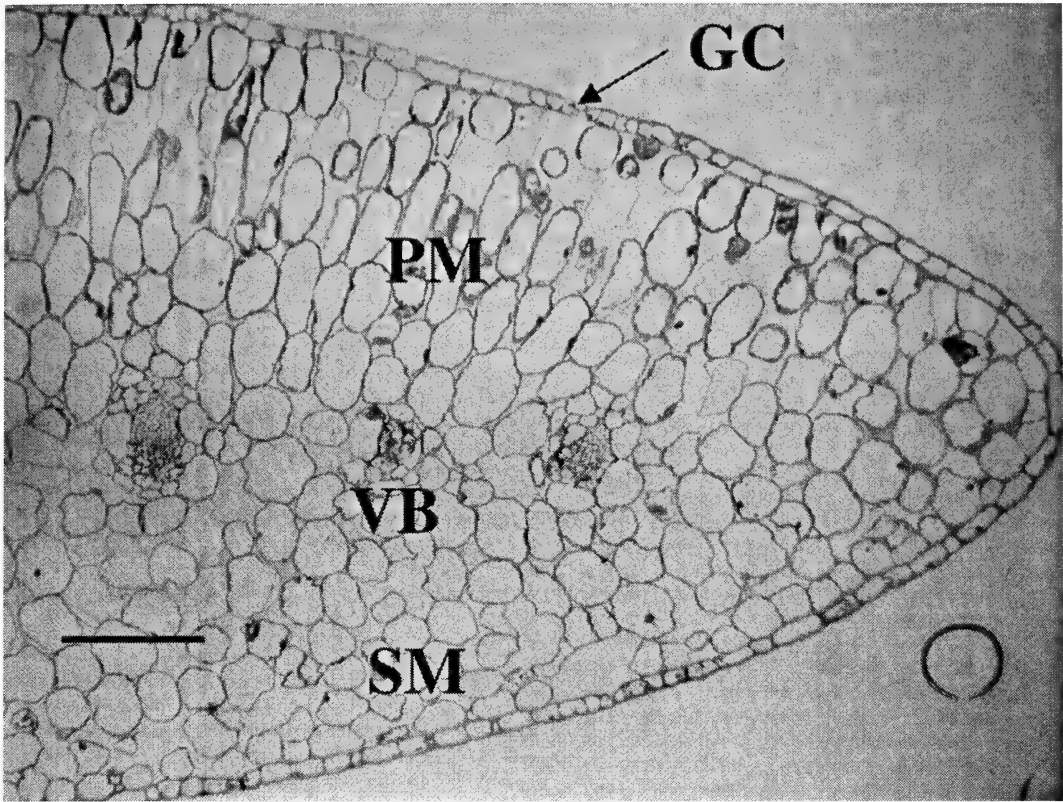
FIGURES 4 and 5. Cross-sections of *Lewisia cotyledon* leaves. Figure 4. Mature leaf cross section, bar = 200 μm. Figure 5. Higher magnification of leaf cross-sections, bar = 100 μm. PM = palisade mesophyll, SM = spongy mesophyll, VB = vascular bundle, GC = guard cell.

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Species	Photosynthetic mode	Percent of mesophyll air space
Peperomia obtusifolia[a]	C_3	27.2
Peperomia camptotricha[a]	CAM-cycling	19.7
Lewisia cotyledon	CAM-cycling	16.8 (4.5)[b]
Peperomia scandens	CAM	6.4

(Gibson 1982). In addition, the mesophyll is generally not well differentiated into palisade and spongy parenchyma layers (Kluge and Ting 1978). Cross sections of *Lewisia* leaves showed no well-organized rows of palisade parenchyma in the mesophyll while typical C_3 plants have a very well organized palisade parenchyma layer. The palisade cells were elongated but the ends of the cells were rounded which is more typical of spongy parenchyma. The palisade cells also contained a very large central vacuole. These anatomical features were similar to the facultative CAM species, *P. afra,* in having a very prominent spongy mesophyll tissue and no well-organized palisade parenchyma (Guralnick 1987).

The percentage of mesophyll airspace found in *Lewisia* places it in the range similar to other CAM and CAM-cycling species, such as *Codonanthe crassifolia* (Focke) C.V. Morton and *Peperomia camptotricha* Miq. which were in the range of 10–20% mesophyll airspace (Smith and Heuer 1981; Gibeaut and Thomson 1989; Guralnick et al. 1986, Table 1). The C_3 *P. obtusifolia* (L.) A. Dietr. had 27% by airspace volume in the spongy mesophyll tissue, which is the CAM-like tissue in *Peperomia* species (Nishio and Ting 1987; Gibeaut and Thomson 1989). The reduced amount of airspace in *Lewisia* compared to a typical C_3 species may be an important component in CAM-cycling by facilitating the capture of CO_2 before it can diffuse out of the leaf. The mesophyll succulence results for *Lewisia* placed it in the range typical of true CAM species such as *P. afra* and *Ceraria fruticulosa* Pearson & E.L. Stephens but the diurnal acid fluctuations were much smaller.

This report indicates that the species *L. cotyledon* shows attributes of the CAM pathway, such as leaf anatomy with primarily a spongy mesophyll present, mesophyll airspace in the range typical of other CAM-cycling species, and a diurnal organic acid fluctuation. The magnitude of the diurnal acid fluctuation places *Lewisia* in the group that performs CAM-cycling. *Lewisia* when compared to other genera showed fewer physiological attributes than other CAM-cycling species. The results presented here correlates with the phylogenetic data presented by Nyananyo (1985) and Hershkovitz and Zimmer (1997) which showed the genus *Lewisia* more closely aligned with the genera of the western North American taxa, *Montia* and *Calyptridium.* Species in these genera show only slightly fleshy, succulent leaves, and low diurnal organic acid fluctuations indicating primarily a C_3 pattern of photosynthesis (Guralnick and Jackson 2001). The results presented in this paper with *Lewisia* would tend to support this hypothesis that anatomical attributes appear earlier with physiological attributes of CAM arising later as indicated by the low levels of PEPCase later which is supported by the phylogenetics of CAM presented by Guralnick and Jackson (2001). In conclusion, the results of this paper indicate that *L. cotyledon* performs CAM-cycling and that CAM is not induced under water-stress conditions.

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THE SIGNIFICANCE OF POPULATION SUCCESSIONAL STATUS TO THE EVOLUTION OF SEEDLING MORPHOLOGY IN *PINUS CONTORTA* VAR. *LATIFOLIA* (PINACEAE)

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Abstract

The objective of this research was to test the hypothesis that the successional role of a plant population, because of its implications for the nature of the selective regime experienced by regeneration cohorts, determines, in part, the course of autecological evolution in a lineage of populations. A provenance study, which involved the raising of seedlings of lodgepole pine (*Pinus contorta* Loudon var. *latifolia*) from seed under uniform conditions in a greenhouse, provided a test of this hypothesis. The seeds came from seral, climax, and persistent lodgepole pine populations indigenous to the Blue Mountains region of northeastern Oregon and southeastern Washington. Data about shoot and root system features, collected at the end of the first season of growth, proved useful in evaluating competitive competence, the relative ability of a plant, or group thereof, to compete successfully for essential resources such as light, water, and mineral nutrients. Analyses of variance and discriminant function analysis facilitated the search for correlations between population successional status and seedling morphology. The total leaf area, photosynthetic potential, degree of subdivision of the root system, and total root length of a typical seedling derived from a seral population are smaller than such quantities for the other population types. In climax populations, seedlings tend to exhibit the largest total leaf areas and total photosynthetic potentials among lodgepole pine seedlings. They are equipped with more elaborate and larger root systems. Despite their exceptional heights, seedlings belonging to persistent populations not only have slightly lower total photosynthetic potentials than those from climax populations, they also possess reduced lateral root densities and total root lengths. Greater competitive competences, with reference to life in the subcanopy, characterize seedlings from climax lodgepole pine populations compared to seedlings from seral or persistent populations. The results of this study support the hypothesis that successional status influences the evolution of autecological attributes in a population lineage.

Forest succession is the undisputed exemplar of vegetation change through time. The formation of a canopy as the crowns of adjacent trees expand in size represents the most consequential structural change occurring during forest succession. In coniferous forests, canopy closure may not occur for over a century after stand establishment (Peet 1981). The appearance of a canopy results in the elimination of an open site and the creation of a subcanopy. Gradual alterations in stand structure and abiotic environmental conditions occur as an open site gives way to a canopied stand.

An open site, though it is an area characterized by physical extremes, is a place where a plant, due to the absence or paucity of other plants with similar requirements, participates in little, if any, competition for essential resources such as light, water, and mineral nutrients. In contrast, the canopy insulates tree seedlings and other inhabitants of the subcanopy from the severe abiotic environmental conditions that prevail on an open site. Nevertheless, because resources are highly accessible to, and vigorously exploited by, the fully developed trees composing the canopy, at least one resource ordinarily limits the survival of subcanopy plants. Con-

sequently, a plant almost invariably must participate in intense intra- and interspecific competition when a resident of the subcanopy. Any new autecological trait appearing through mutation or gene flow that improves the "competitive competence" of a subcanopy plant will increase its fitness, i.e., the likelihood that it will become a part of the canopy and contribute to the genetic constitutions of future generations.

Competitive competence is a relative expression of the ability of a plant, or group thereof, given the features that characterize it (including many aspects of genetics, physiology, anatomy, morphology, and breeding behavior), to compete successfully for those resources that limit maintenance and growth activities. It is an heuristic tool that provides a means of comparing plants according to their abilities to survive, grow, and reproduce under a competitive regime. Competitive competence recalls the general version of the concept of tolerance embraced by most silviculturists during the first half of the twentieth century (e.g., Bühler 1918; Baker 1937, 1950; Toumey and Korstian 1937). Competitive competence permits the comparison of plants growing in naturally complex settings, not under simplified garden, greenhouse, or laboratory conditions; it avoids the artificiality of the tendency to

rank individuals, populations, or species by single-factor tolerances.

To ensure the continued existence of its population lineage (a temporal sequence of conspecific populations related as ancestors and descendants), the members of a population must beget juveniles that are able to compete successfully for resources within the subcanopy, or they must produce propagules that disperse and give rise to individuals capable of surviving, growing, and reproducing in a different location (seed dormancy and cone serotiny may permit the continuity of a population lineage in the absence of emigration). The autecology of a population represents the product of evolutionary history, acting as a phyletic constraint that limits the types of successional role that a population can assume in a given environment. In view of its consequences for regeneration dynamics, successional status certainly contributes significantly to the selective milieu experienced by the members of a population. Consequently, succession potentially influences the course of autecological evolution within a population lineage. Populations of lodgepole pine indigenous to the Blue Mountains region of the Pacific Northwest, which occupy an immense habitat island, represent consummate candidates for studying the relationship between successional status and the evolution of competitive competence.

The successional roles of Blue Mountain lodgepole pine populations. The range of *Pinus contorta* var. *latifolia* (hereafter referred to by its vernacular name "lodgepole pine") encompasses the Rocky Mountains, the Washington Cascades, the area between the Rockies and Coast Range in Canada, and the Blue Mountains. Due to its rapid early growth rate and its tolerance of exposed conditions and poorly developed substrates, lodgepole pine establishes a foothold on many open sites throughout its range (Pfister and Daubenmire 1973; Volland 1985). Hence, lodgepole pine often is a colonizer. In most cases, because of a dearth of nearby seed sources, it becomes only a minor constituent of the stands on these sites. Lodgepole pine adopts a seral role in such situations: It does not regenerate successfully beneath the canopy; species having greater shade tolerances, viz., grand fir (*Abies grandis* (Douglas) Lindley) or subalpine fir (*A. lasiocarpa* (Hook.) Nutt.), replace it in 50–200 years. On some sites, lodgepole pine populations achieve dominance and assume unique successional positions. Pfister and Daubenmire (1973) identified three general successional roles for populations of lodgepole pine in stands that it dominates: (dominant) seral, climax, and persistent. These three population types do not represent different temporal components of a common sere. Rather, each is a particular element of a unique sere. F. C. Hall (USDA Forest Service, unpublished) classified lodgepole pine populations according to successional role in communities that they dominate in the Blue Mountains. Franklin and
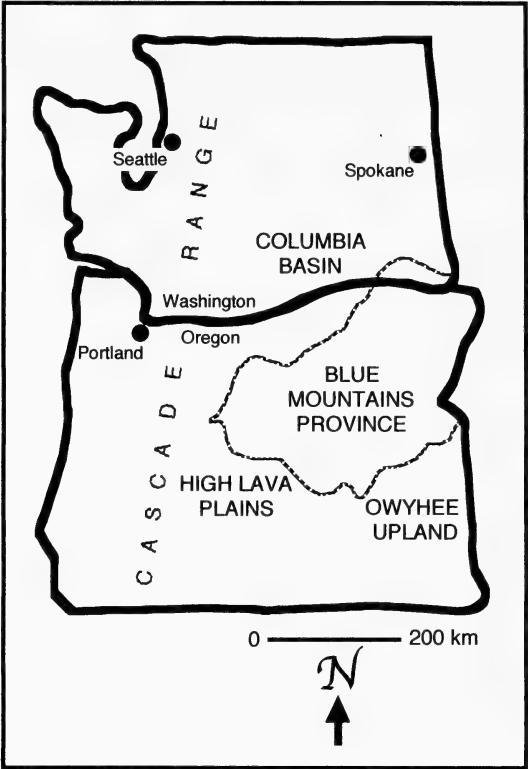

FIG. 1. The Blue Mountains Province, located in northeastern Oregon and southeastern Washington. Modified from Franklin and Dyrness (1988:6).

Dyrness (1988) defined the Blue Mountains Province as the 2.5 million hectare region of mountain ranges and intervening valleys that extends from central Oregon, east of the Cascades, to southeastern Washington (Fig. 1).

Seral populations. Given the availability of a nearby seed source, a lodgepole pine population assumes a seral role in an essentially unidirectional successional sequence upon colonizing an open site characterized by more-or-less moderate abiotic environmental conditions. Lodgepole pine becomes the dominant canopy element because of its rapid early growth rate. In the subcanopy, lodgepole pine seedlings, which represent the offspring of canopy dominants, participate in a futile fight for essential resources with individuals of species that exhibit superior competitive competences (grand fir or subalpine fir). In the absence of stand disturbance, the lodgepole pine population is unable to replace itself in situ. Its adversaries attain dominance in 100–200 years. Perpetuation of the population lineage to which the lodgepole pines belong depends upon local disturbance or the abilities of the seeds of mature individuals to reach, and give rise to viable seedlings on, other (open) sites. As they produce highly vagile propagules and seedlings capable of tolerating the harsh abiotic environmental condi-

tions of open sites, these seral lodgepole pines are exceedingly fit desite their inferior competitive competences.

Climax populations. Because of the exceptional frost resistances and shallow root systems of its seedlings, lodgepole pine is capable of becoming established in a topographic depression where cold air accumulates and the water table often approaches the soil surface. A lodgepole pine population assumes a climax role in a unidirectional, but truncated, sere in such a harsh location. Individuals of other tree species appear on such bitterly cold, and in some cases, periodically inundated, sites only on occasion and in insignificant numbers (though, *Picea engelmannii,* Engelm. is quite abundant on some sites). Even if potentially competing seedlings of other species are present, the superior initial growth rate of lodgepole pine ensures its rapid domination of the canopy. In the subcanopy, the offspring of canopy lodgepole pines generally remain free of competition for essential resources from species having greater competitive competences (grand fir and subalpine fir). Although intraspecific competition is fierce, lodgepole pine regeneration is possible and, in fact, common. Personal observations indicate that climax populations usually contain a mixture of size classes. Seedlings and saplings crowd many light gaps. Stuart et al. (1989) demonstrated that water/mineral nutrient gaps are necessary for seedling establishment in climax populations of *Pinus contorta* Loudon var. *murrayana* (Grev & Balf.) Crichf. in south-central Oregon. Recruitment and the ascendancy of suppressed lodgepole pines into the canopy in the Blue Mountains may require gap formation. Unlike a seral population lineage, a climax population lineage can persist through regeneration in situ, provided that it takes place with sufficient frequency (at intervals no greater than the longevity of lodgepole pine, about 250 years, according to Franklin and Dyrness [1988]), and in adequate quantities. In view of the intense intraspecific competition below a climax lodgepole pine canopy, selection will confer elevated fitnesses on individuals that produce seedlings with greater competitive competences.

Persistent populations. Ten to twenty years after a crown fire destroys a portion of a mature grand fir stand, lodgepole pine seeds originating elsewhere effect colonization of the resulting open site. The lodgepole pine population takes on a persistent role in a cyclic sere on such a site. Due to intense competition with grasses and shrubs (and sometimes grand fir seedlings), the growing lodgepole pines are widely spaced on the site. Nevertheless, because of their rapid early growth rates, they soon form and dominate a canopy. Before long, the subcanopy becomes filled with lodgepole pine seedlings (the progeny of canopy dominants) as well as seedlings having greater competitive competences, i.e., the offspring of grand fir trees that surround

the site. In 60–80 years, the dominant lodgepole pine trees reach maturity (dbh > 14.5 cm) and become susceptible to attack by mountain pine beetles (*Dendroctonus ponderosae*). The deaths of these trees produce a high fuel load within the stand, which inevitably leads to a hot fire 5–10 years later. The fire consumes all live and dead woody material on the site, including canopy members and potential regeneration in the subcanopy. In 10–20 years, the disturbed site becomes suitable for the establishment of lodgepole pine seedlings. Following dispersal from some external seed source, the sequence begins anew. Succession proceeds until a beetle kill and fire again destroy the stand. As a persistent population cannot replace itself in situ, the appearance of lodgepole pine after each fire depends upon seed dispersal from another site. The temporal continuity of a persistent population lineage depends upon the success with which the seedlings of its constituent populations can colonize open sites. Hall's view of the successional role of a persistent Blue Mountain lodgepole pine population is controversial. The details of his proposed successional scenario will likely change once stand development studies are complete. I assume, provisionally, that seed vagility and seedling tolerance of harsh abiotic environmental conditions, not seedling competitive competence, contribute most significantly to the fitness of a persistent lodgepole pine tree.

MATERIALS AND METHODS

Cone collection. A lodgepole pine population represented a dominant canopy element in 61 stands inspected by F. C. Hall (USFS unpublished data) as part of a plant association analysis of the Blue Mountains region. Twenty of these populations proved appropriate for inclusion in this study: In August 1994, each had at least one dominant, codominant, or intermediate lodgepole pine tree that was cone-bearing, accessible, and apparently free of insect damage (Table 1). Using the tripartite scheme introduced above, Hall identified six of these populations as seral (species with superior competitive competences present with height growth rates that exceed those of lodgepole pine trees), seven as climax (topographic depressions; species with superior competitive competences absent), and seven as persistent (species with superior competitive competences present, but lodgepole pine trees exhibit greater height growth rates). Within each successional type, the populations are widely distributed throughout the Blue Mountains with respect to latitude, longitude, and elevation. To reduce the chances that gene flow, not common site-specific selective pressures, might produce a correlation between successional status and competitive competence, I admitted no contiguous populations possessing identical successional roles into this study.

TABLE 1. BLUE MOUNTAIN LODGEPOLE PINE POPULATIONS SAMPLED. The number of participating families indicates those submitted to analyses of variance and discriminant function analysis.

Population	Participating families	Latitude (N)	Longitude (W)	Elevation (m)
Seral populations				
Mount Pisgah	2	44°28'	120°14'	2,100
Little Kelsay Creek	1	44°54'	118°45'	1,900
North Fork Wolf Creek	2	45°08'	118°08'	1,900
Bingham Spring	1	44°30'	120°30'	1,900
Thompson Spring	2	44°28'	120°15'	2,200
Little Phillips Creek	3	45°42'	118°03'	1,700
Climax populations				
Bingham Prairie	2	44°31'	120°32'	1,900
Jackson Creek	2	44°27'	119°58'	1,800
Crowsfoot Creek Edge	1	43°54'	119°30'	1,800
Summit Prairie Edge	2	44°11'	118°30'	1,800
Wickiup Creek	2	44°11'	119°14'	1,800
Ditch Creek Edge	1	45°07'	119°21'	1,600
Myrtle Creek	2	43°59'	119°05'	1,900
Persistent populations				
Stove Spring	2	44°31'	120°33'	1,800
Summit Prairie Slope	3	44°11'	118°30'	1,900
Camp Creek	2	44°03'	119°07'	1,800
Tribble Creek	1	45°10'	119°02'	1,800
Indian Springs Butte	1	44°15'	118°42'	2,100
Dixie Butte	1	44°33'	118°37'	2,000
Winom Creek	1	45°01'	118°38'	1,700

Several assistants and I collected cones from one or more lodgepole pine trees belonging to each population during August 1994. Since minimum distances of 40–50 m separated the sampled trees, each most likely resides within a distinct genetic neighborhood. We recovered a minimum of 50 cones from each tree. We picked the cones off branches removed from each crown by gunshot or through the use of loppers. To maximize the proportion within each family of progeny derived from crosses between members of the same genetic neighborhood, we generally collected cone-bearing branches from the sides of crowns (the infiltration of pollen grains from afar to branches below the tops of crowns probably is limited, especially for trees belonging to seral and climax lodgepole pine populations where crowns frequently are contiguous or overlapping). We used positional criteria so as to collect only those cones that matured in response to pollination events occurring in the spring of 1992. Although most lodgepole pine trees in the Blue Mountains possess nonserotinous cones (Lotan and Critchfield 1990), we were careful to avoid older closed (serotinous) cones. At the time of collection, most cones were light brown in color, which is indicative of ripeness (Krugman and Jenkinson 1974). Many were beginning to open. We stored the cones in paper bags, loosely packed in cardboard boxes, in the open bed of a truck for the duration of the fieldwork (up to four weeks prior to seed extraction).

Seed extraction. Cone processing took place in September 1994 at the Wind River Nursery Seed Extractory operated by the USFS near Carson, Washington. After transferring the cones from the paper bags to loose-weave nylon sacks, we immersed them in hot water (about 60°C) for 4–5 minutes. We dried the cones in a kiln dryer at 35°C for 24 hours. This treatment effectively opened nearly all of the cones. We shook the seeds out of the open cones by use of a manually-driven tumbler. A Clipper cleaner permitted us to partially dewing the seeds and remove debris from each seed lot. We used an x-ray machine and Polaroid film to generate images of the contents of 19–200 seeds per cleaned sample.

Seedling production. After soaking 39 seed lots (each representing a single family) in water for 72 hours, I stratified them without media in polyethylene bags at 2°C for 33 days (Bonner et al. 1974; Krugman and Jenkinson 1974; Owens and Molder 1984; J. McGrath, USDA Forest Service, personal communication). We sowed the seeds immediately after completion of the stratification process in containers in a fiberglass, unheated greenhouse at the University of California, Berkeley. We sowed 2–5 seeds in a 1:1 mixture of sphagnum peat moss and vermiculite in each of 50 Ray Leach Pine Cell Cone-tainers per family. The sowing rate, calculated by reference to the x-ray image of a subsample of seeds produced at the time of seed extraction,

varied in direct proportion to the percentage of filled seeds. We subsequently placed each container in a randomly chosen slot in a cluster of rectangular trays in the center of the greenhouse. We raised over 1,000 lodgepole pine seedlings through a single three-stage season (151 days) under uniform conditions in the greenhouse. To encourage seed germination (1–24 days after sowing), we maintained high air temperatures and relative humidities, suspended a 50% shadecloth near the greenhouse roof to reduce photon flux densities, and kept the growing medium in each container constantly wet. As necessary, we thinned each container to a single seedling. During the free growth phase (25–115 days after sowing), we operated an evaporative cooling system for 12 hours per day, illuminated the seedlings with fluorescent lights for 18 hours per day, and injected a Plantex 20:20:20 macro- and micronutrient solution (100 ppm of nitrogen) into the irrigation system during every other watering (about once each week). We created drought stress conditions and terminated the use of daylength extension lights at the beginning of the budset stage (116–151 days after sowing). Throughout this final period of seedling growth, we used an exhaust fan for 24 hours per day to encourage lower temperatures and relative humidities, and we halved the nitrogen content of each fertilizer application (50 ppm of nitrogen).

Collection of data on seedling morphology. Theoretical predictions and empirical evidence suggest that, regardless of sibling relatedness and heritability, an acceptable approximation of a family mean for a given quantitative morphological feature is obtainable by sampling 10–20 progeny (Brady unpublished). Consequently, within three weeks of termination of the growth period (i.e., the end of the bud-set stage), we harvested ten randomly-chosen seedlings per family on which terminal resting buds had developed and acquired information for 12 distinct morphological attributes. A description of each trait appears in Table 2.

Statistical procedures. Following the recommendations of Gould and Johnston (1972) for identifying patterns of geographical variation within and among species, I adopted different approaches, viz., analyses of variance and discriminant function analysis, in my attempt to discover a correlation between lodgepole pine seedling morphology and population successional status. The analysis of variance (ANOVA) furnishes a way to evaluate the observed differences among three or more (statistical) population means (Winer 1971; Tabachnick and Fidell 1983; Lindman 1992; Bogartz 1994). In the context of the present investigation, successional status functions as the sole independent variable with three levels, or groups (seral, climax, and persistent). The morphological features act as dependent variables. Discriminant function analysis includes an array of multivariate techniques that

TABLE 2. DESCRIPTIONS OF 12 ATTRIBUTES PERTAINING TO SHOOT AND ROOT SYSTEM MORPHOLOGY ASSESSED FOR LODGEPOLE PINE SEEDLINGS ON WHICH TERMINAL RESTING BUDS HAD DEVELOPED WITHIN 151 DAYS OF GROWTH IN A GREENHOUSE.

SHL (shoot length)

The distance between the cotyledonary node and the base of the terminal resting bud on the main stem as measured with a ruler to the nearest millimeter.

STC (stem caliper)

The maximum diameter of the main stem at its midlength (*SHL*/2), as measured with a vernier caliper to the nearest 0.025 mm.

NPL (number of needle-like primary leaves)

The number of needle-like primary leaves attached to the main stem, disregarding cotyledons.

NSS (number of axillary short-shoots)

The number of axillary short-shoots attached to the main stem.

NLS (number of axillary long-shoots)

The number of axillary long-shoots attached to the main stem.

BLL (blade length)

Pertaining to the intact and fully developed primary leaf closest to the midlength of the main stem (*SHL*/2), the distance between the base and tip of the leaf blade along its midrib, as measured with a ruler to the nearest millimeter.

TPC (taproot caliper)

The maximum diameter of the taproot at its midlength (actually, half the distance between the cotyledonary node and the tip of the taproot), as measured with a vernier caliper to the nearest 0.025 mm.

NLR (number of lateral roots)

The number of lateral (secondary) roots attached to the proximal half of the taproot (the region between the cotyledonary node and the midlength of the taproot).

LRL (lateral root length)

The length of the lateral root attached closest to the midlength of the taproot, as measured with a ruler to the nearest millimeter.

NTR (number of tertiary roots)

The number of tertiary (absorbing) roots connected to the lateral root that is attached closest to the midlength of the taproot (we considered a tertiary root and all of its branches, if present, as a single unit).

SHB (shoot biomass)

The weight of the air-dried shoot system (epicotyl), as obtained with an electronic balance to the nearest 0.01 g.

ROB (root biomass)

The weight of the air-dried root system (hypocotyl), as obtained with an electronic balance to the nearest 0.01 g.

make use of a set of independent variables to discover the dimensions along which the differences among groups are greatest, to test the statistical significance of those differences, to predict group

TABLE 3. THE MEAN AND STANDARD DEVIATION OF THE FAMILY MEAN OF EACH OF 12 MORPHOLOGICAL FEATURES OF LODGEPOLE PINE SEEDLINGS BY SUCCESSIONAL CLASS FOR 34 FAMILIES. Units of measurement appear in parentheses. All numbers were rounded to two digits to the right of the decimal point for display purposes.

	SHL (mm)	STC (mm)	NPL	NSS	NLS	BLL (mm)	TPC (mm)	NLR	LRL (mm)	NTR	SHB (g)	ROB (g)
					seral (total number of families = 11)							
mean =	58.36	1.87	106.86	4.66	2.02	35.56	0.66	27.20	92.38	26.49	35.56	28.05
sd =	8.17	0.11	10.41	4.10	0.64	2.70	0.11	2.62	5.33	3.79	7.40	4.69
					climax (total number of families = 12)							
mean =	61.00	1.95	117.54	1.48	2.26	36.68	0.65	29.66	98.23	29.14	37.13	33.33
sd =	8.00	0.09	16.35	1.91	0.23	1.32	0.12	2.44	7.74	4.01	3.82	2.47
					persistent (total number of families = 11)							
mean =	72.26	1.87	115.23	2.60	2.26	37.14	0.69	26.68	95.42	27.69	38.75	32.01
sd =	7.58	0.12	11.86	3.25	0.23	1.87	0.07	3.08	6.90	3.77	3.12	3.87

membership, and to interpret the (biological) meaning of each dimension (Kendall and Stuart 1966; Lachenbruch 1975; Gnanadesikan 1977; Karson 1982; Tabachnick and Fidell 1983; Reyment et al. 1984; Morrison 1990). In this study, successional status is the dependent variable with three groups (seral, climax, and persistent). Morphological attributes act as independent variables. I performed all quantitative analyses for this study on a MacIntosh Quadra 950 using JMP 3.1 application software or programs written by myself and executed with the Microsoft QuickBASIC 1.00B Interpreter.

RESULTS AND DISCUSSION

I calculated the means and standard deviations of family means by successional class (seral, climax, and persistent) on each of 12 morphological traits for a total of 390 lodgepole pine seedlings (39 families). Examination of these statistics as well as histograms depicting the frequency distributions of families for these features (not shown) indicated that five families (one seral, two climax, and two persistent) represent outliers. I made no further use of the data for these five families. Table 3 gives summary statistics on each of the 12 morphological features by successional class for the remaining 34 families. The mean of family means on three of the attributes each exhibits very little variation among successional classes: NLS (number of axillary long-shoots), TPC (taproot caliper), and SHB (shoot biomass). Consequently, I withdrew them from further statistical consideration.

Analyses of variance. The validity of the results of a series of ANOVAs depends upon the assumption that the scores on a particular dependent variable within each group are approximately normally distributed, and upon the assumption that each group possesses a common variance on a given dependent variable. I evaluated the normality assumption separately for the nine morphological traits within each of the three successional classes in two ways: I examined a histogram showing the distri-

bution of family means, which facilitated the visual detection of skewness, and I tested the null hypothesis that this distribution is normal using the Shapiro-Wilk W-statistic. An assumption of normality was supported for eight of the attributes in every class ($\alpha = 0.05$). The distribution of one seedling feature, NSS (number of axillary short-shoots), exhibited severe positive skewness in the climax and persistent groups. Therefore, I did not probe NSS further using ANOVA. I performed four different statistical tests (O'Brien's, Brown-Forsythe, Levene F, and Bartlett's tests) to check the homogeneity of variance among the three successional classes for each of eight morphological characteristics. None of the tests detected statistically significant ($\alpha = 0.05$) differences in variance among groups for any of these traits.

Eight ANOVAs revealed that the differences among group means are statistically significant ($\alpha = 0.05$) for three morphological attributes: SHL (shoot length), NLR (number of lateral roots), and ROB (root biomass). In each case, t-tests identified the particular group differences responsible. The results of the significant tests appear in Table 4.

Year-old seedling shoots are, on average, longer in families derived from persistent populations (mean SHL = 72.26 mm) than in families belonging to either seral or climax populations (58.36 mm and 61.00 mm, respectively). However, no real difference in seedling shoot length exists between seral and climax groups. The t-tests detected significant differences in the number of lateral roots between seral and climax and between climax and persistent groups. In fact, the largest mean number of lateral roots per seedling (mean NLR = 29.66) characterize climax families. However, no evidence exists of a genuine difference in the number of lateral roots between seral and persistent families (27.20 and 26.68, respectively). The biomasses of seedling root systems are significantly smaller in seral families (mean ROB = 28.05 g), but the climax and persistent groups are not statistically dis-

TABLE 4. RESULTS OF SIGNIFICANT ($\alpha = 0.05$) ONE-WAY ANALYSES OF VARIANCE AND T-TESTS OF THE DIFFERENCES AMONG SUCCESSIONAL CLASSES IN MEAN VALUES ON EIGHT LODGEPOLE PINE SEEDLING TRAITS. df = degrees of freedom, SS = sum of squares, MS = mean square. I rounded all numbers to two digits to the right of the decimal point for display purposes.

	SHL (shoot length)				
Source	df	SS	MS	F	P
successional status	2	1208.22	604.11	9.62	0.00
error	31	1946.33	62.79		
^{t}seral:persistent = 4.14 df = 20	P = 0.00				
^{t}climax:persistent = −3.46 df = 21	P = 0.00				

	NLR (number of lateral roots)				
Source	df	SS	MS	F	P
successional status	2	58.82	29.41	3.98	0.03
error	31	228.83	7.38		
^{t}seral:climax = 2.33 df = 21	P < 0.03				
^{t}climax:persistent = 2.58 df = 21	P < 0.02				

	ROB (root biomass)				
Source	df	SS	MS	F	P
successional status	2	171.28	85.64	6.08	0.01
error	31	436.90	14.09		
^{t}seral:climax = 3.43 df = 21	P = 0.00				
^{t}seral:persistent = 2.16 df = 20	P < 0.04				

tinguishable on the basis of this trait (33.33 g and 32.01 g, respectively).

A series of ANOVAs yields the maximum amount of information about the importance of each attribute to the determination of group affiliation only if none of those traits covary. A matrix of Pearson product-moment correlation coefficients (Table 5) indicates that, in fact, every pair of morphological attributes is, to some degree, correlated. Thus, the claim that differences among successional classes on the mean values of SHL, NLR, and ROB are statistically significant incorrectly implies that successional status affects three independent phenomena. A closer examination of the relationship between seedling morphology and successional status demands a multivariate perspective.

Discriminant function analysis. Justification of a multivariate normality assumption (within each group, the sampling distribution of the mean on each independent variable and all linear combina-tions of them exhibit normality) is a prerequisite for the use of discriminant function analysis. With small, unequal sample sizes (as in this study), validation of the multivariate normality assumption is largely a matter of judgment. By discarding the attribute NSS (number of axillary short-shoots), shown previously to possess a highly skewed distribution within each successional class, the validity of the assumption of multivariate normality is likely.

A discriminant function analysis of 34 lodgepole pine family means on each of eight morphological characteristics, which accounts for about 68.2% of the total variation in seedling morphology, created two discriminant functions (Table 6). The first function effectively ordinates all three successional classes by partitioning approximately 66.5% of the variation among successional classes to achieve group separation (Fig. 2). The second discriminant function appropriates about 33.5% of the variation

TABLE 5. CORRELATION MATRIX OBTAINED BY COMPUTING PAIRWISE PEARSON PRODUCT-MOMENT CORRELATION COEFFI-CIENTS ACROSS ALL THREE SUCCESSIONAL CLASSES FOR EIGHT MORPHOLOGICAL FEATURES.

	SHL	STC	NPL	BLL	NLR	LRL	NTR	ROB
SHL	1.0000							
STC	−0.0049	1.0000						
NPL	0.3757	0.1093	1.0000					
BLL	0.2631	0.0554	0.2300	1.0000				
NLR	−0.3149	0.4287	0.0759	−0.0122	1.0000			
LRL	0.3808	0.2128	0.2941	0.4289	0.0791	1.0000		
NTR	0.1109	−0.0596	0.1189	0.4347	0.3571	0.6601	1.0000	
ROB	0.3650	0.2161	0.3255	0.4426	0.2874	0.4326	0.4246	1.0000

TABLE 6. DISCRIMINANT FUNCTION ANALYSIS OF A DATA SET CONSISTING OF 34 LODGEPOLE PINE FAMILY MEANS ON EIGHT FEATURES PERTAINING TO SEEDLING MORPHOLOGY.

Discriminant function	standardized discriminant function coefficients							
	SHL	STC	NPL	BLL	NLR	LRL	NTR	ROB
1	−1.0138	0.1790	0.2367	−0.2789	0.0476	0.5094	−0.0759	0.2698
2	0.3117	0.1089	0.2082	0.1081	0.2483	0.0600	−0.0327	0.5586

Comparison of predicted and actual group membership

Predicted group membership	Actual group membership		
	Seral	Climax	Persistent
Seral	8	1	0
Climax	1	11	2
Persistent	2	0	9

Discriminant function	Loading matrix							
	SHL	STC	NPL	BLL	NLR	LRL	NTR	ROB
1	−0.7301	0.3860	0.0434	−0.1769	0.5557	0.1818	0.1757	0.0939
2	0.5628	0.3780	0.5765	0.4998	0.3649	0.5492	0.4326	0.8950

among successional classes to distinguish seral from the other groups (Fig. 2).

A jackknife technique failed to expose any unusually large Mahalanobis' distances (the distances in multivariate space from family means to their group centroids); and plots of standardized family scores for the seral, climax, and persistent groups revealed roughly equal dispersions. These findings verify the absence of multivariate outliers and sup-
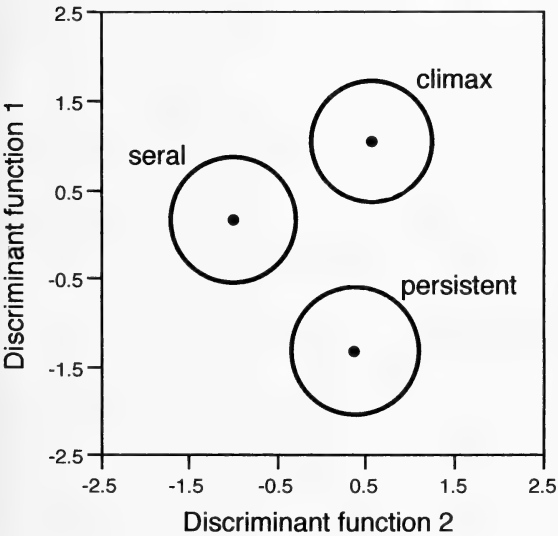
FIG. 2. The location of each of three lodgepole pine successional classes in multivariate space as defined by a discriminant function analysis of eight attributes pertaining to seedling morphology. Each axis consists of standardized scores on the indicated discriminant function. A dot marks each group centroid (mean standardized discriminant function score). The area enclosed by a circle corresponds to the 95% confidence region around a given centroid.

port the assumption of homogeneous variance-covariance matrices, which validate the use of discriminant function analysis in this study. Two results confirm the statistical significance of this multivariate inquiry: Firstly, an approximate F-ratio justified rejection of the null hypothesis that the centroids associated with the three successional classes are equal. Secondly, in a comparison of actual group memberships and those based on posterior probabilities obtained from Mahalanobis' distances, 82% of the 34 family predictions proved correct (Table 6). The large value (0.73) of the associated Kappa statistic, which measures the agreement between predicted and actual group affinity, connotes that the results of the present discriminant function analysis are, indeed, very reliable.

I referred to the loading matrix (Table 6) to explain the differences among seral, climax, and persistent population types on each of the two discriminant functions. Following statistical convention, I deemed only those loadings of at least 0.50, which implies an overlap in variance of about 25% between an independent variable and a discriminant function, as eligible for interpretation.

A seedling's growth polarity. The first, and most information-laden, discriminant function, or dimension of variation in seedling morphology, reflects a change in the pattern of asset allocation, not the overall amount of growth. In morphometric terms, most of the variation among successional classes, as explained by the first dimension, is attributable to the alteration of seedling "shape", not "size". This finding differs markedly from the results of most multivariate morphometric studies, which hopelessly confound the genetic determination of form and phenotypic plasticity, and where the first axis of variation corresponds to a generalized size dimension (Reyment et al. 1984). All of the inde-
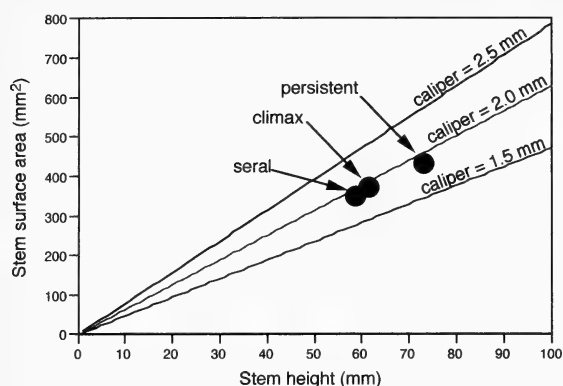
Fig. 3. Surface area of a cylindrical stem as a function of stem caliper and height. The three points indicate the average stem surface areas of lodgepole pine seedlings derived from seral, climax, and persistent populations.

pendent variables that contribute substantially to a size dimension must exhibit discriminant function coefficients, correlations among themselves, and loadings of like sign (Jolicoeur and Mosimann 1960; Reyment et al. 1984). In the present case, the two morphological attributes having the largest absolute loadings on the first discriminant function (SHL and NLR) possess discriminant function coefficients, correlations, and loadings of opposite sign. The first dimension of variation clearly portrays an anisotropic pattern of change in seedling growth among seral, climax, and persistent lodgepole pine populations.

The trait SHL (shoot length) represents a measure of the total amount of seedling height growth during the first season of development, or a height growth rate. Internode elongation, the primary component of height growth, may lead to the production of new leaves in regions of higher photon flux densities, it may move existing leaves into sunlight, and it tends to reduce self-shading by increasing the distances among appendages attached to the stem (e.g., Horn 1971; Hallé et al. 1978; Fisher 1986; Givnish 1986, 1988, 1995; Sakai 1986; Kohyama 1987; Küppers 1989). Since their epicotylar stems remained green during the first season of development, height growth via internode elongation may further contribute to the carbon economies of lodgepole pine seedlings by promoting stem photosynthesis (see Nilsen 1995). The total green stem surface area provides a means of comparing the stem photosynthetic potentials of different groups of seedlings. As the epicotylar stems observed in this study lacked taper, I calculated the surface area of a stem by assuming that it is cylindrical in shape. The surface area of a stem increases with both height and caliper (Fig. 3). Because long-shoots were relatively small and nearly constant in number across all lodgepole pine seedlings (NLS in Table 3), the exclusive application of a simple cylindrical model to the main stem furnishes an adequate com-

parative measure of the total stem photosynthetic potential. The three points in Fig. 3 mark the average main stem surface areas for the three lodgepole pine successional classes (based on mean STC and mean SHL from Table 3). Due to their exceptional heights (mean SHL = 72.26 mm), seedlings from persistent families possess the greatest stem photosynthetic potentials. Seedlings from seral and climax populations have comparable stem photosynthetic potentials (mean SHL = 58.36 mm and 61.00 mm for seral and climax groups, respectively).

NLR (number of lateral roots) is the second morphological attribute making a large contribution to the differentiation of successional classes along the initial dimension of variation. As it provides an estimate of the degree of branching, or subdivision of the root system, NLR relates the thoroughness with which a seedling can extract water and mineral nutrients from a given volume of soil (Fitter 1985, 1991, 1994; Caldwell and Richards 1986). While only its tip functions in uptake, a lateral root provides a "platform" for numerous absorbing tertiary roots. Because the most efficient zone of absorption occurs near the tip of any root, the total number of root tips in a specified volume of soil acts as a measure of the absorptive capacity of a root system (Kramer and Kozlowski 1960; Caldwell and Richards 1986). Imagine a lodgepole pine seedling root system that is completely embedded in a cylindrical mass of soil. The height and vertical centerline of the cylinder correspond to the length and position of the taproot, and its radius equals the length of a lateral root. All lateral roots are identical in length, and each possesses the same number of attached tertiary roots. The following equation gives the total number of root tips characteristic of the root system per mm^3 of soil:

$$T = \frac{P + l_{taproot}d_{laterals} + l_{taproot}d_{laterals}l_{lateral}d_{tertiary\ roots}}{\pi(l_{lateral})^2 l_{taproot}}$$

(1)

where P is the number of taproot tips (usually, $P = 1$); $l_{taproot}$ is taproot length; $d_{laterals}$ is a density, the number of lateral roots produced per unit length of taproot; $l_{lateral}$ is the length of a lateral root; and $d_{tertiary\ roots}$ is the density of tertiary roots along a lateral root. The product $l_{taproot}d_{laterals}$ gives the total number of lateral root tips. The product $l_{taproot}d_{laterals}l_{lateral}d_{tertiary\ roots}$ yields the total number of tertiary root tips. The denominator is the volume of the reference cylinder of soil. Based on estimates of P (1), $l_{taproot}$ (160 mm) and $d_{tertiary\ roots}$ (0.29 per millimeter of lateral root length) from this study (all are essentially constant among the seedlings analyzed), Fig. 4 presents T as a function of lateral root density for three different lateral root lengths. The number of root tips composing a root system per unit volume of soil increases in response to both an augmentation in the number of lateral roots attached to
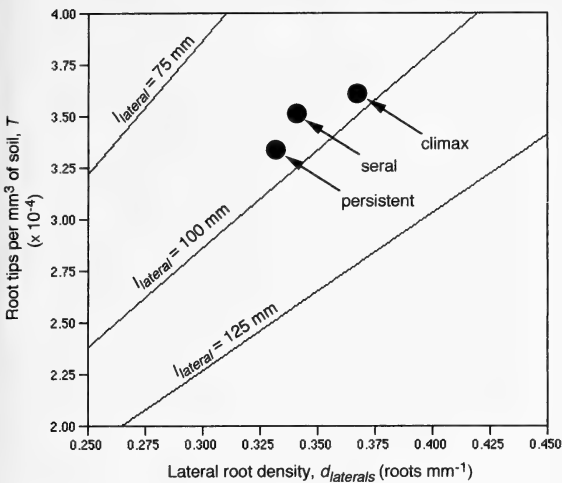
FIG. 4. The number of root tips composing a lodgepole pine seedling root system per mm³ of soil (T) as a function of lateral root density ($d_{laterals}$) and lateral root length ($l_{lateral}$). The three labelled points indicate the average values of T for seedlings belonging to the seral, climax, and persistent groups.
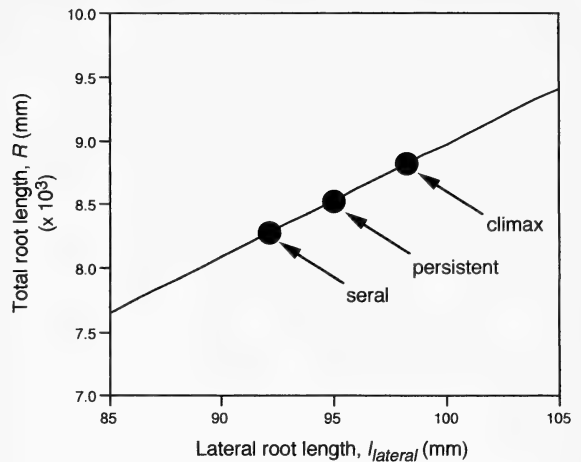

FIG. 5. Total root length (R) as a function of lateral root length ($l_{lateral}$). The three labelled points mark the average total root lengths for the three lodgepole pine successional classes.

the taproot and a decrease in the lengths of lateral roots (the radius of the cylindrical mass of soil). The three points in Fig. 4 indicate the average values of T for lodgepole pine seedlings belonging to the seral, climax, and persistent groups ($d_{laterals}$ is twice the value of mean NLR from Table 3 divided by a taproot length of 160 mm; $l_{lateral}$ is mean LRL from Table 3). Bearing in mind the simplifying assumptions associated with the calculation of T, the absorptive capacities of seedlings from climax populations only slightly exceed those of seral seedlings, though, given their longer lateral roots, the former may have access to water and mineral nutrients from larger volumes of soil than either seral or persistent seedlings. Seedlings derived from persistent populations possess distinctively lower absorptive capacities, due mainly to the production of fewer lateral roots (mean NLR = 27.20, 29.66, and 26.68 for seral, climax, and persistent families, respectively).

A seedling's resource acquisition potential. Discriminant function analysis identified a second, less explanatory, dimension that highlights the variation in the ability of Blue Mountain lodgepole pine seedlings to obtain essential resources from their surroundings. It utilizes information about overall seedling size and the sizes of individual organs involved in the interception/uptake of light, water, and mineral nutrients to separate the three successional classes in multivariate space. In accord with the interpretation of the second dimension as a size vector, all five morphological attributes with high loadings (≥ 0.50) on the second discriminant function (SHL, NPL, BLL, LRL, and ROB) possess standardized discriminant function coefficients, corre-

lations among themselves, and loadings of similar sign (Tables 5 and 6).

ROB (root biomass), the morphological characteristic having the greatest loading on the second discriminant function, grades the overall size of the seedling root system. ROB does not convey information about shape, i.e., the pattern of subdivision of the root system. Instead, it incorporates, and inevitably confounds, two aspects of development: total root length (the sum of the lengths of all roots) and average root caliper. Consider a lodgepole pine seedling in which all lateral roots are identical in length, each lateral root possesses the same number of attached tertiary roots, and all tertiary roots are equal in length. Under these conditions, the following equation expresses the total root length in mm:

$$R = l_{taproot} + n_{laterals}l_{lateral}$$
$$+ n_{laterals}l_{lateral}d_{tertiary\ roots}l_{tertiary\ root} \qquad (2)$$

where $l_{taproot}$ is taproot length; $n_{laterals}$ is the number of lateral roots attached to the taproot; $l_{lateral}$ is the length of a lateral root; $d_{tertiary\ roots}$ is a density, the average number of tertiary roots that arise per unit length of lateral root; and $l_{tertiary\ root}$ is the length of a tertiary root. The quantity $n_{laterals}l_{taproot}$ is the sum of the lengths of all lateral roots. The product $n_{laterals}l_{taproot}d_{tertiary\ roots}l_{tertiary\ root}$ represents the sum of the lengths of all tertiary roots. The results of this study supplied constant values for $l_{taproot}$ (160 mm), $n_{laterals}$ (55.8, twice the mean of 34 family means on NLR from Table 3), and $d_{tertiary\ roots}$ (0.29 mm⁻¹). The approximate median of the range of mature tertiary root lengths of forest trees reported by Sutton and Tinus (1983) provided a reasonable value for $l_{tertiary\ root}$ (2.0 mm). Figure 5 shows that the total length of a lodgepole pine seedling root system (R) increases in direct proportion to lateral
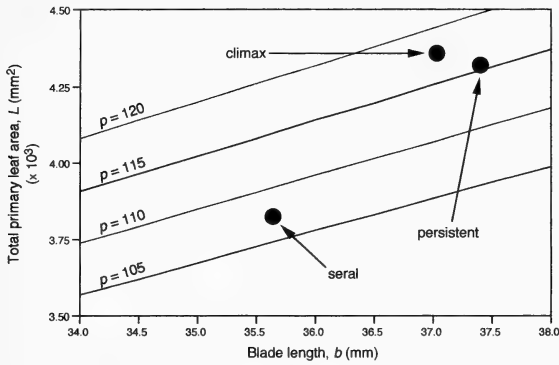
FIG. 6. Graph of total primary leaf area (L) for various values of p (number of primary leaves) and b (blade length). The three labelled points correspond to the total primary leaf areas of average lodgepole pine seedlings belonging to the seral, climax, and persistent groups.

root length ($l_{lateral}$). The three points in Figure 5 denote the values of R for typical seedlings belonging to the seral, climax, and persistent groups (based on mean *LRL* from Table 3). The typical specific root lengths (calculated from R and mean *ROB* in Table 3) associated with seral, climax, and persistent seedlings are 296.06, 264.64, and 244.62, respectively. An increase in total root length allows the root system to explore the soil and locate unexploited resources (Fitter 1985, 1991, 1994; Caldwell 1987, 1994). Seral seedlings possess the smallest total root lengths. The total root lengths of seedlings from climax populations surpass those of seedlings from other population types. Hence, superior abilities to find water and mineral nutrients within the soil distinguish climax seedlings.

Three shoot system attributes (*SHL, NPL,* and *BLL*) help to isolate the seral group along the second dimension of variation (Table 6). As discussed above, *SHL* (shoot length) reflects, among other things, the surface area of the green epicotylar stems. Leaf morphology significantly influences the amount of light that a plant can intercept for use in photosynthesis (e.g., Taylor 1975; Givnish 1979, 1988; Givnish and Vermeij 1976). Specifically, *NPL* (number of needle-like primary leaves) and *BLL* (blade length) jointly provide information about total primary leaf area, a useful comparative measure of leaf photosynthetic potential among lodgepole pine seedlings. All primary leaves analyzed in this study were dorsiventrally flattened and approximately rectangular in outline. By assuming that the leaves are identical in length and width (1 mm), the following equation gives the total primary leaf area (the sum of the single-sided areas of all primary leaves) in mm² of a lodgepole pine seedling:

$$L = pb \qquad (3)$$

where p is the number of primary leaves and b is blade length. As shown in Figure 6, L increases

with both blade length and number of leaves. Based on the mean values of *NPL* and *BLL* from Table 3, the three points in Figure 6 betoken the total primary leaf areas of average lodgepole pine seedlings belonging to the seral, climax, and persistent groups. Since they produce fewer and shorter primary leaves, seedlings derived from seral populations are distinguished by having substantially smaller total primary leaf areas than seedlings of other successional affinities. The average total primary leaf area of climax seedlings barely exceeds that of persistent seedlings. Despite their long blades, the modest production of primary leaves by persistent seedlings restricts their total primary leaf areas.

The competitive competences of Blue Mountain lodgepole pine seedlings. In a comparative sense, seedlings from seral lodgepole pine populations in the Blue Mountains are unremarkable in exhibiting no conspicuous preference for either shoot or root system growth (Fig. 2; Tables 3 and 6). However, they are notably smaller than seedlings belonging to climax and persistent populations in overall and individual organ size (Fig. 2; Tables 3 and 6). Due to restricted height growth and the production of few and small primary leaves, relatively low photosynthetic potentials characterize seral seedlings (Figs. 3 and 6). Although seedlings derived from seral populations manufacture modest numbers of root tips per unit volume of soil (Fig. 4), root extension growth is anemic. Their small total root lengths (Fig. 5) imply that seral seedlings can explore only limited regions of the soil for water and mineral nutrients. Compared to the juvenile members of climax populations, seedlings taken from seral populations possess morphological traits that would place them at distinct competitive disadvantages wherever light or soil resources are scarce, i.e., within the subcanopy (even in a light or water/mineral nutrient gap). With reference to life in the subcanopy, seedlings from seral lodgepole pine populations exhibit relatively low competitive competences.

Allocation patterns in climax seedlings favor root system elaboration over shoot growth (Fig. 2; Tables 3 and 6). In addition, in terms of both general size and the sizes of organs involved in light interception and water/mineral nutrient uptake, climax populations have the largest seedlings of all successional groups (Fig. 2; Tables 3 and 6). Climax seedlings exhibit unimpressive stem photosynthetic potentials (Fig. 3). However, compared to seedlings from seral and persistent populations, climax seedlings exhibit superior primary leaf photosynthetic potentials, principally as the result of the fabrication of greater numbers of leaves (Fig. 6). Seedlings from climax populations produce relatively large numbers of root tips per unit volume of soil (Fig. 4) as well as long roots (Fig. 5). Climax seedlings have morphological traits, especially those reflect-

ing their abilities to find and absorb extremely scarce soil water and mineral nutrients, that would give them clear advantages over other lodgepole pine seedlings within the subcanopy. Seedlings from climax populations possess greater competitive competences, as regards subcanopy life, than those from seral or persistent populations.

Development in seedlings from persistent lodgepole pine populations is aimed at expansion of the shoot system to the detriment of root growth (Fig. 2; Tables 3 and 6). Persistent seedlings are roughly comparable in size to those belonging to climax populations, but considerably larger than seedlings from seral populations (Fig. 2; Tables 3 and 6). Because of their incredible heights, the stem photosynthetic potentials of persistent seedlings far exceed those of seedlings from other population types (Fig. 3). However, since they produce fewer leaves, the primary leaf photosynthetic potentials of persistent seedlings are slightly lower than those of seedlings from climax populations (Fig. 6). Although moderate root lengths characterize seedlings from persistent lodgepole pine populations (Fig. 5), they bear relatively few root tips per unit volume of soil (Fig. 4). Persistent seedlings have "stunted" root systems that impair their abilities to locate and extract water and mineral nutrients from the soil. Hence, they probably could not survive competition with climax seedlings in a canopied stand, except, perhaps, in a water/mineral nutrient gap. Seedlings derived from persistent lodgepole pine populations display intermediate competitive competences, as concerns life in the forest subcanopy.

Possible sources of unexplained variation in seedling morphology. Error variation accounts for 31.8% of the total variation among 34 Blue Mountain lodgepole pine family means on eight attributes pertaining to seedling morphology considered by discriminant function analysis. Here, error variation is equivalent to the variation among families within successional classes. Discriminant function analysis cannot identify specific sources of error variation. However, several factors, including both experimental inadequacies and evolutionary forces, represent plausible causes. While failings in the experimental procedure undermine the assumption that all observed morphological variation reflects underlying genetic variation, selection, gene flow, and drift may yield error variation with a genetic basis.

A lack of spatial uniformity in the environmental conditions within the greenhouse could account for some proportion of error variation. During development, the seedlings were randomly distributed within the cluster of trays on the greenhouse benches. They were not blocked by family or successional class. Unless it produced skewed distributions of counts or measurements, this factor would benignly promote within-family variability, not variation among family means within a succession-

al group. No visible spatial pattern of variation in above-ground growth performance had emerged by the time of harvest. Therefore, any unintended systematic variation in photon flux density, watering, fertilizer application, temperature, or relative humidity probably played a relatively minor role in the generation of morphological variation among families.

In forested settings, lodgepole pine seedlings usually form ectomycorrhizae with various basidiomycetes and ascomycetes following the development of tertiary roots (Castellano and Molina 1989). Because we sowed the seeds in artificial growing medium, the seedlings used in this study could become naturally ectomycorrhizal only through wind dispersal of spores from fruiting bodies on infected trees near the greenhouse. As ectomycorrhizae influence the growth of lodgepole pine by enhancing the uptake of water and mineral nutrients (Cline and Reid 1982; Ekwebelam and Reid 1983), the differential infection of seedlings could generate error variation. In fact, careful, but non-microscopic, examinations failed to provide evidence (fungal mantles or trailing hyphae) of a single infected seedling.

Diagnostic mistakes also could produce error variation. Since the order in which we diagnosed the seedlings was random, inaccuracies in counting and measuring would tend to increase within-family variability rather than error variation (unless they rendered skewed data). To minimize systematic diagnostic inconsistencies, the same individual assessed a given morphological attribute for all seedlings.

Selective pressures induced by environmental variables unrelated to successional status (e.g., climate, soil parent material composition, topographic position, and elevation) doubtless are partly responsible for the creation of error variation. Although they probably are not independent of population successional status, such symbiotic relationships as herbivory, parasitism, and mutualism may influence the evolution of seedling morphology in ways not directly affecting the outcome of competition for resources (e.g., Coley 1983). In the most general sense, the observed pattern of genetic variation in lodgepole pine seedling morphology represents a compromise among phyletic constraints, concurrent, but often conflicting, selective pressures imposed by numerous environmental factors, gene flow, and drift.

Conclusions. The purpose of this research was to carry out a test of the hypothesis that the successional role of a plant population, because of its implications for the nature of the selective regime experienced by regeneration cohorts, determines, in part, the course of autecological evolution within a lineage of populations. The results demonstrate that, in accordance with predictions deduced from the hypothesis, a rather strong and statistically sig-

nificant correlation exists between a heritable pattern of variation in competitive competence, as revealed by seedling morphology, and the successional status (seral, climax, or persistent) of a lodgepole pine population in the Blue Mountains region of northeastern Oregon and southeastern Washington.

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ESTUDIO ANATÓMICO DE SWALLENIA (POACEAE: ERAGROSTIDEAE: MONANTHOCHLOINAE), UN GÉNERO MONOTÍPICO DE NORTE AMÉRICA

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Resumen

Swallenia Soderstr. & H. F. Decker es un género endémico de California, Estados Unidos de América, extremadamente raro, tiene afinidades taxonómicas inciertas y se encuentra en peligro de extinción. Se presentan observaciones de morfología, anatomía foliar y micromorfología de la lema. Muestra una estructura "Cloridoide", anatomia Kranz tipo PCK o PEP-ck y subtipo X_yMS+. La lámina foliar, vista en sección transversal, es nodular debido a que ambas superficies, abaxial y adaxial, tienen surcos profundos. El clorénquima es continuo entre haces vasculares contiguos. Las células de parénquima incoloro, comunes en la subtribu Monanthochloinae, están ausentes. La vaina externa del haz es redonda. La epidermis, en vista superficial, carece de papilas y los estomas están confinados a los surcos y están cubiertos por aguijones y una célula "papiliforme" intercostal. Las células cortas costales se distribuyen en largas hileras de hasta 15 células o más. Los caracteres observados en la lema tienen correlación con los de la lámina foliar, sin embargo, no muestran un patrón definido. Se describe su hábitat y se hacen algunas consideraciones adaptativas. Las características anatómicas no apoyan la ubicación del género *Swallenia* en la subtribu Monanthochloinae.

Abstract

Swallenia Soderstr. & H. F. Decker is a rare genus, with uncertain taxonomic affinities, endemic to California, USA and endangered. Morphology, leaf blade anatomy and lemma micromorphology are presented. It shows a "Chloridoid" structure, Kranz anatomy PCK or PEP-ck type and X_yMS+ subtype. The leaf blade, as viewed in transverse section, is nodular because abaxial and adaxial surfaces have deep grooves. Chlorenchyma is continuous between adjacent vascular bundles. Colourless parenchyma cells, that are common in the Monanthochloinae subtribe, are absent. Outer bundle sheath is round. In the epidermis, as seen in surface view, papillae are absent and stomata occur in the grooves and are obscured by prickles and an intercostal "papilliform" cell. Costal short cells are arranged in rows to 15 cells or more. Lemma micromorphology characters are correlated to those of the leaf blade, but they do not show a characteristic pattern. Habitat and adaptative considerations are described. The anatomical characters do not support the placement of *Swallenia* genus as belonging to Monanthochloinae subtribe.

Swallenia Soderstr. & H. F. Decker, con su única especie (*S. Alexandrae* (Swallen) Soderstr. & H. F. Decker) es una planta rizomatosa, perenne; con la lígula en una línea de pelos; inflorescencia una panícula contraída y escasa; glumas casi tan largas como la espiguilla, membranosas, 7–11 nervios; lemas 5–7 nervios, villosas en los márgenes, mucronadas, pálea villosa en el margen.

Swallenia fue colectado por Annie M. Alexander y Louise Kellogg en Mayo de 1949 en la localidad del Valle de Eureka, Condado de lnyo en California. Swallen (1950) reconoció algunos rasgos únicos y lo describió como *Ectosperma,* un género monotípico. El nombre genérico se invalidó porque ya se había usado, en 1903, para un género algal. Más tarde, Soderstrom y Decker (1963) lo renombraron en honor a Jason R. Swallen (1903–1991), distinguido agrostólogo americano que contribuyó de manera destacada al conocimiento de las gramíneas del Nuevo Mundo, y designaron como especie tipo a *Swallenia alexandrae* (Swallen) Soderstr. y H. F. Decker.

Swallen (1950) consideró este género como miembro de la tribu Festuceae pero con base en características (glumas tan largas como las espiguillas) afines a la tribu Aveneae. Pilger (1954) también lo ubicó en la tribu Festuceae junto con los géneros *Melica* L., *Schizachne* Hack., *Lycochloa*

Samuels, *Vaseyochloa* Hitchc., *Anthochloa* Nees y Meyen, *Neostapfia* Davy y *Ramosia* Merr. No obstante, con base en caracteres morfológicos y aquellos anatómicos generados por Metcalfe (1960), Stebbins y Crampton (1961) lo incluyeron en la tribu Monanthcohloinae (=Aeluropodineae) al lado de géneros como *Aeluropus* Trin., *Distichlis* Raf., *Monanthochloë* Engelm., *Jouvea* Fourn. y *Vaseyochloa*. Gould y Shaw (1983) reconocieron la tribu Aeluropodeae e incluyeron los géneros *Distichlis, Allolepis* Soderstr. y H. F. Decker, *Monanthochloë* y *Swallenia*. Diversos autores como Clayton y Renvoize (1986), Peterson et al. (1995, 1997) y Watson y Dallwitz (1992) reconocen a *Swallenia alexandrae* como integrante de la subtribu Monanthochloinae y tribu Eragrostideae. Peterson et al. (1995) proponen una clasificación tribal para las Eragrostídeas del nuevo Mundo y reconocen la subtribu Monanthochloinae con seis géneros americanos (*Distichlis, Jouvea, Allolepis, Monanthochlöe, Reederochloa* y *Swallenia*) excepto *Aeluropus* que se distribuye en el Viejo Mundo.

Observaciones previas de la anatomía foliar de *Swallenia* (Gómez y Koch, 1993) y micromorfología de la lema de Monanthochloinae (Gómez 1998) revelaron ciertas características notables y únicas. Estas características anatómicas, sus afinidades taxonómicas inciertas y su distribución restringida combinadas con el pobre conocimiento acerca de su hábitat, morfología, micromorfología de lema, etc., hacen de *Swallenia* un género importante y merecedor de un estudio exhaustivo y detallado. Este género esta probremente representado en los herbarios y, hasta ahora, se conocen solamente los ejemplares tipo. Las primeras colectas datan de los años 50's y el género se estableció en 1963. No se registran más colectas sino hasta el 22 de Mayo de 1976 y posteriormente hasta el 30 de Marzo de 1986. Esta última es una fotografía de la planta en su medio natural y está depositada en la colección del Herbario de la Universidad de California (UC). El objetivo de este trabajo es proveer información amplia y detallada que servirá para entender las afinidades taxonómicas del género y posteriormente evaluar sus relaciones filogenéticas.

MATERIALES Y METODOS

Se revisaron 23 especimenes provenientes de los herbarios CAS, RSA, UC y US (Cuadro 1), acrónimos según Holmgren et al. (1990). Para la anatomía foliar se consideraron láminas basales y de su parte media se tomó un fragmento de 1 cm. Para las observaciones con microscopía óptica, se hicieron preparaciones anatómicas de la epidermis abaxial en vista superficial y la estructura interna vista en sección transversal siguiendo las técnicas de raspado directo y secciones manuales de Metcalfe (1960) y Gómez y Koch (1998). El montaje se hizo en jalea glicerinada, sin tinción. Para las observaciones al microscopio electrónico de barrido

CUADRO 1. COLECTORES Y COLECCIONES DONDE ESTÁN DEPOSITADOS IOS ESPECIMENES EXAMINADOS.

Swallenia alexandrae (Swallen) Soderstr. y H. F. Decker
Annetta carter 2784, 8.Jun.1950, topotipo (RSA, UC, US).
Annie M. Alexander y Louise Kellogg 5655, 24.May.1949, isotipo (UC).
Christopher Davidson 4015, 22.May.1976 (RSA).
Douglas Powell s.n., 21.Abr.1952, topotipo (UC, US).
D. E. Anderson. 2406, 6.Abr.1963 (UC).
D. W. Taylor s.n., 17.Nov.1979 (UC).
Jack L. Reveal y Arlene H. Reveal 37, 13.May.1962, topotipo (RSA, UC).
James D. Morefield y Douglas H. McCarty 3297, 30.Mar.1986, topotipo (RSA, UC).
John C. Roos 6352, 6355 y 6365, 13.May.1955, topotipo (CAS, RSA, UC).
John & Lucille Roos 6175, 28.Jun.1954. topotipo (CAS, RSA, UC).
John & Lucille Roos 6467, 21.Jun.1955 (RSA).
John y Lucille Roos 6320, 10.Abr.1955 (RSA, UC).
Mary de Decker 1457, 2.Abr.1961, topotipo (RSA).

(MEB), las muestras se trataron previamente con cloroformo por 2–6 horas para remover la cutícula y algunas impurezas.

La micromorfología de la lema se estudió en ejemplares de herbario con ayuda del MEB. Las muestras se tomaron del primero y segundo flósculo de espiguillas maduras y se trataron previamente con cloroformo de 2–4 horas para remover la cutícula. Después de lavar con agua, se montaron en portaobjetos, se llevaron a un baño de aluminio y se tomaron las fotomicrografias con un microscopio Hitachi S-2460N. En algunos casos (Figs. 3, 4A–B) se hizo el baño en oro y se empleo un microscopio JEOL.

Para las descripciones de anatomía se siguió la terminología propuesta por Ellis (1976, 1979) con algunas modificaciones. Las ilustraciones de anatomía foliar, para microscopía óptica, se hicieron con ayuda de una cámara clara. La epidermis abaxial está orientada de tal forma que el eje longitudinal de la lámina aparece en posición horizontal en la ilustración y el ápice hacia la derecha.

RESULTADOS

Swallenia Soderstr. & H. F. Decker, Madroño 17: 88. 1963. Tipo: *Swallenia alexandrae* (Swallen) Soderstr. and H. F. Decker.

Este género es endémico, extremadamente raro e interesante, de afinidades inciertas y adaptado a sobrevivir en sitios secos y arenosos. Se han generado diferentes criterios acerca de su ubicación taxonómica lo que ha hecho dificil el entendimiento de sus afinidades filogenéticas.

Morfología (Fig. 1). Planta perenne, rizomatosa, rizomas robustos. Culmos amacollados, erectos, 10–60 cm de altura (formando colonias o masas
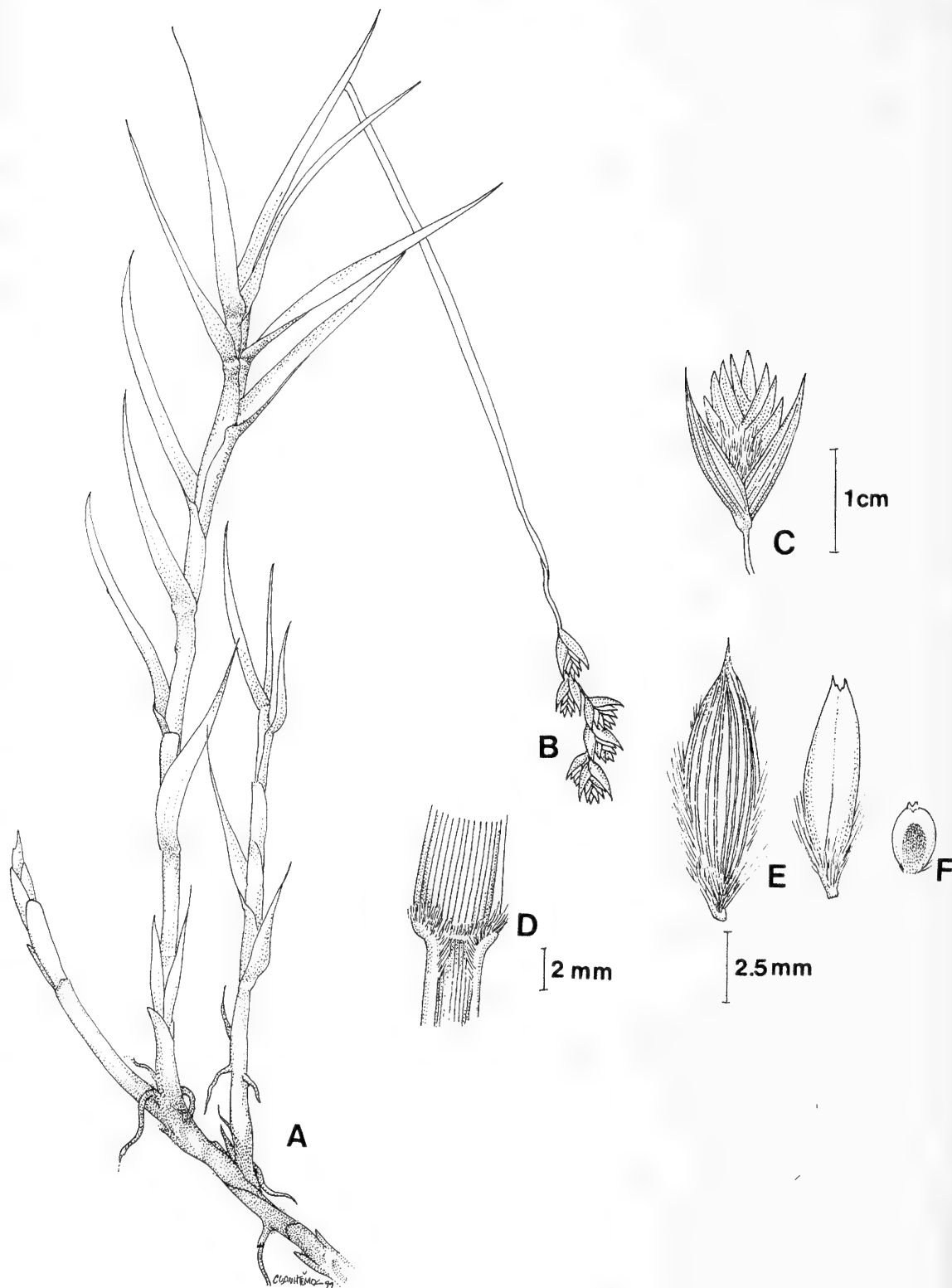
FIG. 1. *Swallenia alexandrae* (Swallen) Soderstr. & H. F. Decker. A. Hàbito de la planta. B. Panícula. C. Espiguilla. D. Lígula. E. Flósculo. F. Cariopsis. (Ilustración de *Reveal & Reveal* 37, UC).
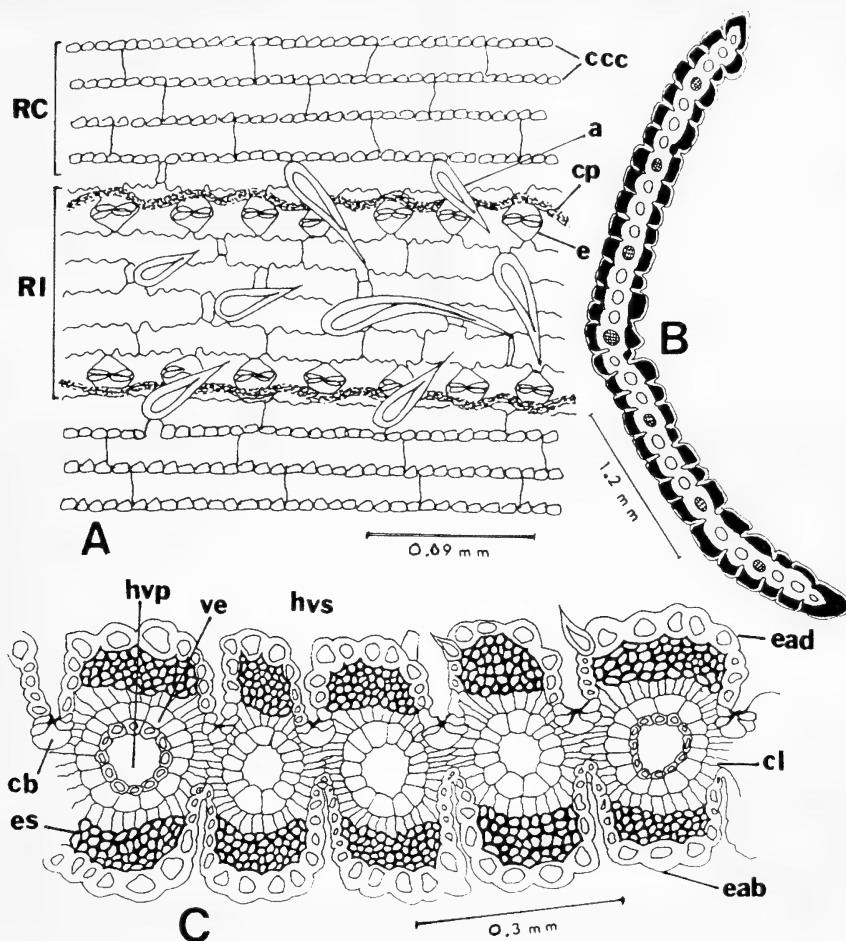
FIG. 2.   *Swallenia alexandrae* (Swallen) Soderstr. & H. F. Decker. Lámina foliar vista con microscopio óptico (Ilustración de *D. Powell s/n, US*). A. Epidermis abaxial. B y C. Sección transversal. RC = región costal, RI = región intercostal, a = aguijón, cb = células buliformes, ccc = célula corta costal, cl = clorénquima, cp = célula "papiliforme", e = estoma, eab = epidermis abaxial, ead = epidermis adaxial, es = esclerénquima, hvp = haz vascular primario, hvs = haz vascular secundario, ve = vaina externa del haz.

extensas de hasta dos metros de diámetro), cespitosos, pilosos. Vainas más largas que los entrenudos, márgenes lisos, ciliadas (villosas en la garganta y el collar), las maduras basales fibrosas, perennes (en la base de las plantas), color ocre-amarillentas. Articulación vaina-lámina conspicua. Lígula una línea de pelos, 1.0–1.5 mm de largo. Aurículas ausentes. Lámina foliar linear; plana a convoluta; conspicuamente nervada, nervios 30–40 en la superficie abaxial; pulverulenta; rígida; punzante; ápice atenuado; 3–13 cm de largo; 3–5 mm de ancho. Inflorescencia una panícula contraída; 4–10 cm de largo; 0.5–1.0 cm de ancho; ramas ligeramente adpresas; exerta o parcialmente incluida en las vainas superiores; eje principal escabroso; ramas primarias adpresas al eje principal; pedicelos pilosos, escabrosos. Desarticulación arriba de las glumas, lema y palea caen como una unidad. Callo piloso. Espiguillas (5)10–15(20) mm de largo, casi tan largas como anchas, solitarias, lateralmente comprimidas,

hialinas a verde-amarillentas, ovadas, pedicelos 0.5–1.0 mm de largo. Glumas tan largas como la espiguilla o ligeramente más largas, lisas, glabras, membranosas a coriáceas. Primera gluma 6–7 nervios, 10 mm de largo, ápice acuminado. Segunda gluma, 7–11 nervios, 9–10 mm de largo, ápice acuminado. Raquilla conspicuamente marcada entre los flósculos, entrenudos 0.3–0.5 mm de largo, pubescentes a escabrosos. Flósculos 3–7 por espiguilla. Flósculos estériles presentes, arriba de los flósculos fértiles. Lema entera; 7–8 mm de largo; sin arista; papirácea; densamente pilosa a villosa; 5–7 nervada, nervios conspicuos y pilosos. Pálea pilosa; 5–6 mm de largo; papirácea; 3–4 nervada, nervios conspicuos; márgenes no envolviendo el fruto, ciliados, lisos. Lodículas truncadas. Estambres 3. Anteras 2.0 mm de largo, rojizas a púrpura. Estigmas 2. Cariopsis redondeado a ovoideo elipsoidal, a veces dorsoventralmente comprimido, con las bases de los estilos persistentes. Cariopsis con las bases
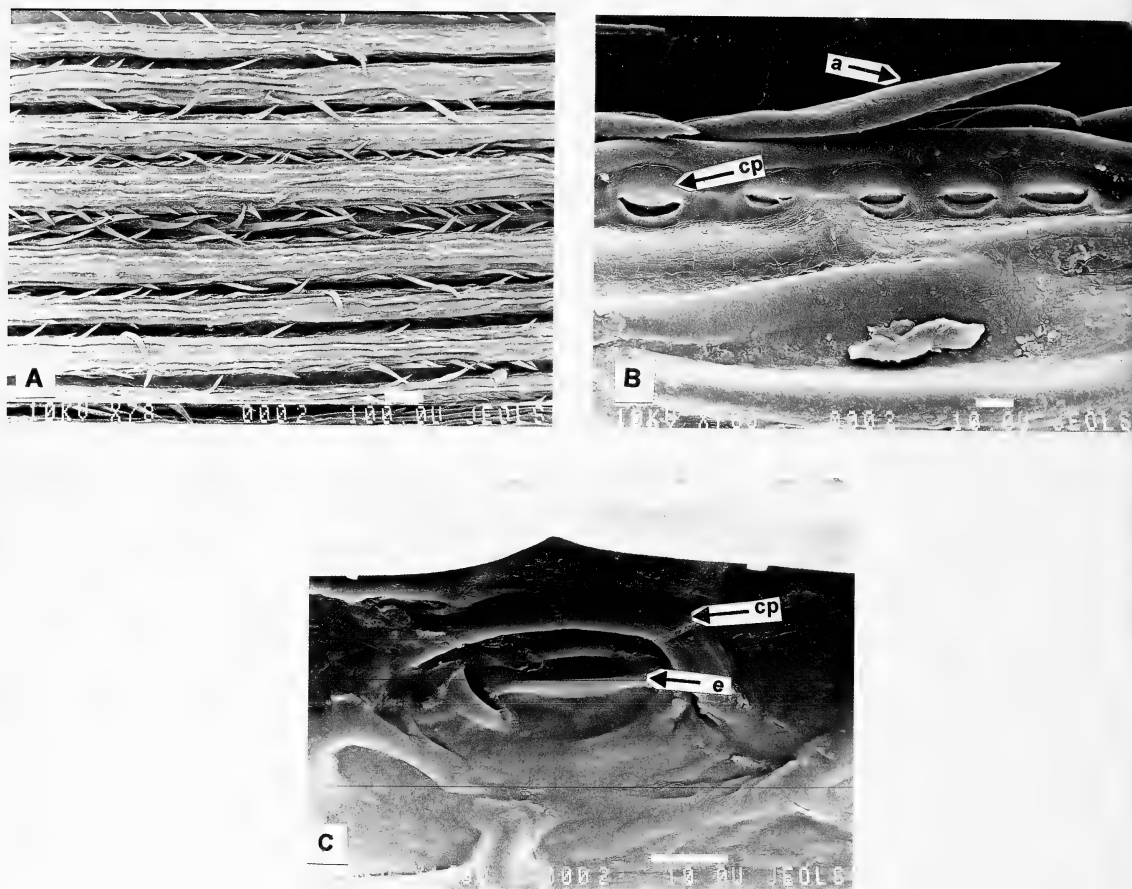
Fig. 3. *Swallenia alexandrae* (Swallen) Soderstr. & H. F. Decker. Lámina foliar vista al microscopio electrónico de barrido (Ilustración de *D. Powell s/n, US*). A. Epidermis abaxial. B y C. Epidermis adaxial. a = aguijón, cp = célula papiliforme, e = estoma.

de los estilos relativamente cortos. Número básico de cromosomas X = 10, 2n = 20.

Anatomía

Sección transversal (Figs. 2B, C). Involución de la lámina en forma de "V", muy amplia, nodular. Cara abaxial con surcos profundos y costillas pronunciadas; ápice de las costillas cuadrado, redondeado, o plano. Cara adaxial con surcos profundos y costillas pronunciadas; ápice de las costillas cuadrado, redondeado, o plano. Razón profundidad del surco:grosor de la lámina 0.4–0.5. Haces vasculares 30–32; usualmente haces vasculares primarios y secundarios, a veces dos terciarios alternando con los haces vasculares primarios. Vaina externa del haz completa, redondeada en todos los haces vasculares. Extensión de la vaina externa del haz ausente. Esclerénquima abaxial y adaxial; copioso; el abaxial en grandes hebras frente a los haces vasculares, 10–14 células de ancho y 3–6 células de alto; el adaxial en grandes hebras sobre los haces vasculares, 8–15 células de ancho y 4–8 células de alto; ausente sobre los haces vasculares terciarios cuando

éstos existen. Esclerénquima abaxial intercostal ausente. Clorénquima radial alrededor de los haces vasculares; sus células alargadas y estrechas; continuo entre haces vasculares sucesivos. Células incoloras ausentes. Células buliformes en grupos adaxiales discretos, regulares; célula central ligeramente inflada; 0.05 mm de largo; casi a la mitad del grosor de la lámina o más corta.

Epidermis abaxial (Figs. 2A, 3A) Regiones costal e intercostal bien diferenciadas. Células largas de 20 μm de largo; paredes anticlinales horizontales sinuosas en la región costal y onduladas en la intercostal; paredes periclinales con punteaduras simples abundantes, conspicuas. Estomas abundantes, 15 estomas por campo visual; rómbicos (vistos en superficie), a veces en domo; en 1–2 hileras hacia los márgenes de la región intercostal; usualmente cubiertos por una célula "papiliforme" intercostal, a veces ocultos por aguijones costales e intercostales. Células cortas costales en hileras largas (de hasta 15 células), cuadradas a redondeadas. Células cortas intercostales ausentes; cuando presentes entonces solitarias, altas y estrechas, rara vez
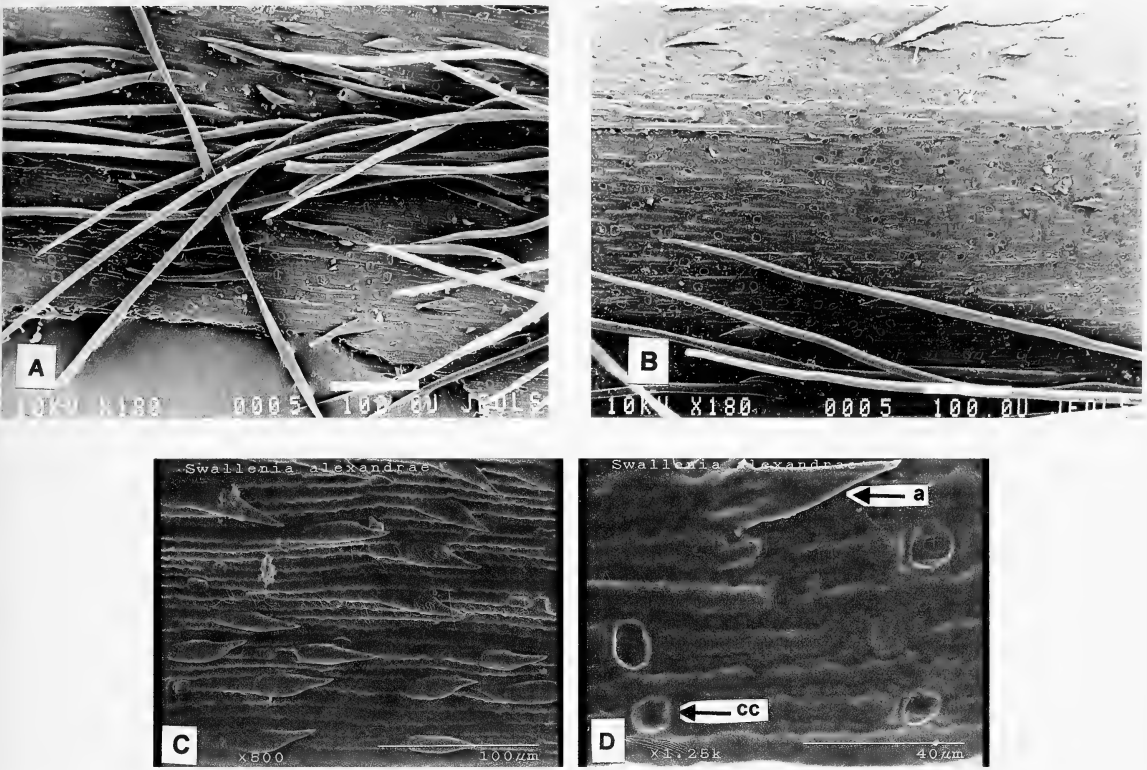
FIG. 4.   *Swallenia alexandrae* (Swallen) Soderstr. & H. F. Decker. Micromorfología de lema vista al microscopio electrónico de barrido. A y B. Parte basal (Ilustración de *A. Carter 2784, UC*). C y D. Parte media (Ilustración de *D. Powell s/n, US*). a = aguijón, cc = célula corta.

cuadradas. Cuerpos de sílice siempre en la región costal y ausentes en la intercostal; redondeados, cuadrados, o en forma de silla de montar; 3.0–4.5 μm de largo. Papilas ausentes. Aguijones abundantes, usualmente intercostales, cubriendo los estomas, a veces costales. Micropelos no vistos. Macropelos ausentes.

Micromorfología de la lema (Fig. 4). Base de la lema pilosa. Regiones costal e intercostal no diferenciadas. Células largas con paredes anticlinales horizontales fuertemente onduladas a sinuosas. Papilas ausentes. Células cortas abundantes, usualmente solitarias, a veces en pares, altas y estrechas, cuadradas o redondeadas. Cuerpos de sílice redondeados a ligeramente cuadrados. Aguijones abundantes. Micropelos no vistos. Macropelos ausentes.

DISTRIBUCIÓN

Norteamérica. Nativa del Nuevo mundo. Sólo se le conoce de los Estados Unidos de América. Crece en las dunas arenosas de Eureka al sureste de California (Fig. 5). Especie endémica del Valle de Eureka, en el Condado de Inyo, en California.

Hábitat

Swallenia alexandrae es una planta xerofítica y se desarrolla en vertientes o laderas bajas de dunas arenosas, en sitios secos y a una altitud entre los 2900 y 3400 m. Crece en grandes colonias o masas de hasta un metro o más de diámetro y profundamente incrustada en arenas silíceas (Henry 1979). Se le encuentra asociada con *Chaetadelpha wheeleri, Cleome sparsifolia, Coldenia plicata, Dalea polyadenia, Dicoria clarkae, Ligodesmia juncea, Oenothera deltoides* y *Stanleya pinnata* spp. *Inyoensis,* entre otras.

Estatus de Conservación

Esta especie se encuentra en las listas rojas de la Unión Internacional de Conservación de la Naturaleza (Walter y Gillett 1998). Se considera en peligro de extinción en los Estados Unidos y especie rara en California (Smith y York 1984; Hickman 1996).

DISCUSIÓN Y CONCLUSIONES

La ubicación de *Swallenia alexandrae,* en la subtribu Monanthochloinae, hasta ahora habia sido apoyada con base en su morfología externa. Los estudios anatómicos en este género son escasos. Metcalfe (1960) y Watson y Dallwitz (1992) señalan parcialmente algunas caracteristicas de la lámina foliar. Esta investigación proporciona información anatómica amplia, adiciona algunos aspectos
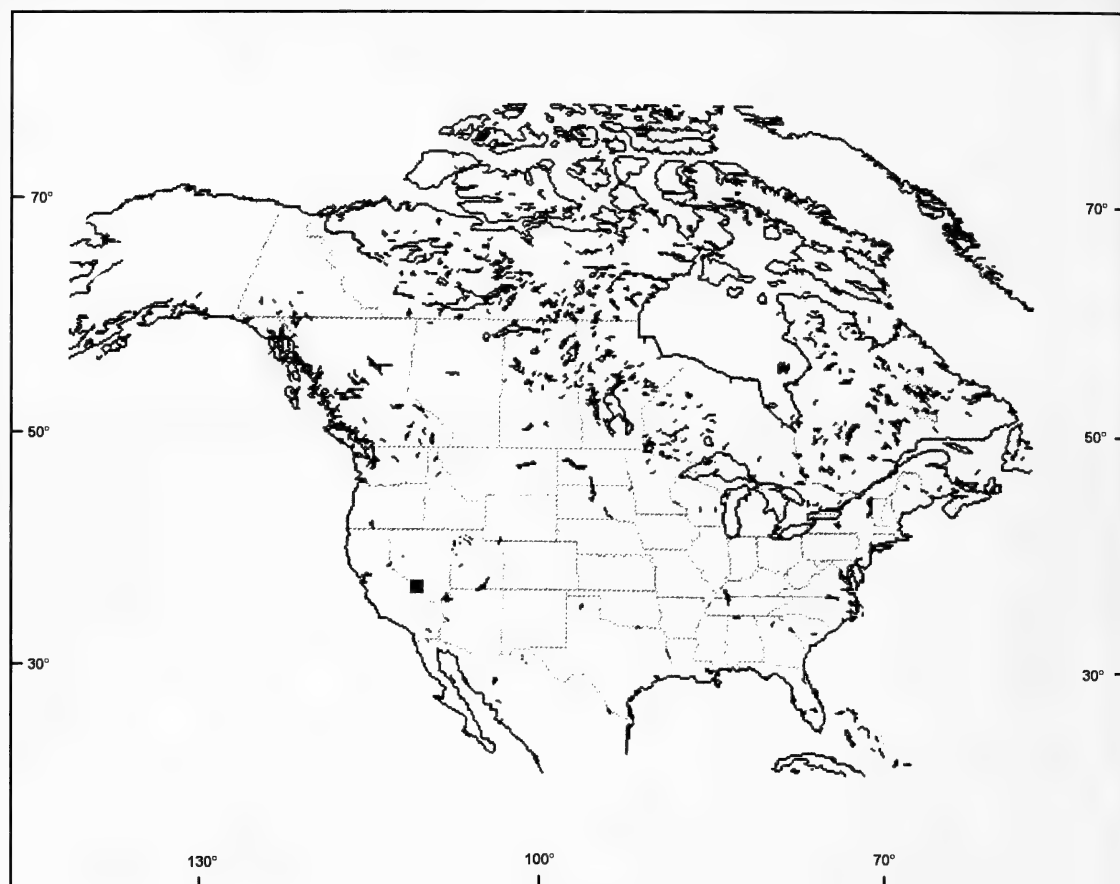
Fig. 5. Mapa de distribución de *Swallenia alexandrae* (Swallen) Soderstr. y H. F. Decker.

de la micromorfología de la lema y detalles importantes que permiten entender mejor sus afinidades.

Swallenia comparte algunos caracteres morfológicos con los otros miembros de la subtribu Monanthochloinae, tales como la lema papirácea y con 5–7 nervios y la lígula definida por una línea de pelos. No obstante, este género se diferencia del resto de los componentes, por poseer cariopsis con las bases de los estilos persistentes y cortos y porque sus flores son perfectas o hermafroditas. Esta observación coincide con la opinión de Peterson et al. (1997).

La información citológica se reduce al conocimiento del número cromosómico. La especie tiene un número cromosómico X = 10 (*Peterson* et al. 1997) o el diploide 2n = 20 (Hickman 1996). Este número coincide con el de algunos de los géneros restantes de la subtribu.

Las características anatómicas que se manifiestan en la sección transversal de la lámina foliar de *Swallenia alexandrae* evidencian una estructura "cloridoide" según lo propuesto por Brown (1958). Presenta todos los haces vasculares rodeados por una vaina externa parenquimática conspicua, provista de grandes cloroplastos, abundantes y dis-

tintos de los del clorénquima. Los haces vasculares primarios poseen además una vaina interna fibrosa, conspicua, que rodea completamente al xilema y floema. El clorénquima se compone de células de pared delgada y está dispuesto de manera radial alrededor de los haces vasculares. El número máximo de células clorénquimáticas, existentes entre haces vasculares contiguos, es de 2 a 3, considerándose bajo (Hattersley y Watson 1975). Estos caracteres permiten además inferir que, por tener esta estructura anatómica denominada Kranz, *Swallenia* pertenece a las plantas C_4, es decir, que en su vía fotosintética sigue el ciclo de Hatch y Slack (1966). Esta estructura anatómica Kranz es conocida como tipo PCK y la especie es PEP-ck, Tiene una vaina del haz doble y cloroplastos especializados dispuestos de manera centrífuga, esto es, están hacia la pared celular externa de la célula de la vaina Kranz. Asimismo, es evidente el subtipo anatómico X_yMS+ por la presencia de células (de la vaina interna) entre los elementos del metaxilema y la vaina parenquimática (Kranz), sobre todo en los haces vasculares primarios (Brown 1975, 1977; Ellis 1977; Hattersley y Watson 1976; Watson y Dallwitz 1992).

CUADRO 2. CARACTERES QUE DISTINGUEN AL GÉNERO *SWALLENIA* DEL RESTO DE LA SUBTRIBU MONANTHOCHLOINAE. HV = haces vasculares, VE = vaina externa del haz.

CARACTERES	Swallenia	Jouvea	Distichlis	Allolepis	Aeluropus	Reederochloa	Monanthochloe
MORFOLOGIA							
Flores	hermafroditas	unisexuales	unisexuales	unisexuales	hermafroditas	unisexuales	unisexuales
Cariopsis con bases de los estilos persistentes	presentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes
ANATOMIA FOLIAR							
Células cortas costales en hileras de 15 células	presentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes
Célula papiliforme que cubre el estoma	presente	ausente	ausente	ausente	ausente	ausente	ausente
Papilas intercostales	ausente	presentes	presentes	presentes	presentes	presentes	presentes
Aguijones	abundantes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes
Forma de micropelos	ausentes	claviforme	claviforme	claviforme	claviforme	claviforme	claviforme
Lámina vista en sección transversal	nodular	no-nodular	no-nodular	no-nodular	no-nodular	no-nodular	no-nodular
Surcos de la lámina	abaxiales y adaxiales	adaxiales	adaxiales	adaxiales	adaxiales	adaxiales	adaxiales
Esclerénquima	grandes hebras	trabas o hebras	trabas	trabas o hebras	trabas	trabas o hebras	trabas o hebras
Arrego de las células incoloras	ausentes	en columna	en columna	en columna	en columna	en columna	en columna
Forma de los HV	redonda	ovada	ovada	ovada	ovada	ovada	ovada
Forma de la VE del haz	redonda	ovada	ovada	ovada	ovada	ovada	ovada
clorénquima entre HV contiguos	continuo	interrumpido	interrumpido	interrumpido	interrumpido	interrumpido	interrumpido
MICROMORFOLOGÍA DE LEMA							
Aguijones	abundantes	escasos	escasos	escasos	escasos	ausentes	ausentes
Papilas	ausentes	presentes	presentes	presentes	presentes	presentes	presentes
Base	villosa	no-villosa	no-villosa	no-villosa	no-villosa	no-villosa	no-villosa
Cuerpos de sílice	abundantes	frecuentes	abundantes frecuentes	escasos	frecuentes	escasos	escasos

La lámina foliar es nodular por la presencia de costillas pronunciadas y surcos profundos en ambas superficies (Fig. 2C). La presencia de los surcos profundos y los estomas y aguijones (Fig. 3A, B) confinados a dichos surcos, son características que permiten, a la planta, su adaptación al hábitat extremo donde crece. Las grandes hebras de esclerénquima y los surcos profundos confieren a la lámina rigidez y evitan su colapso.

En la epidermis no se observaron micropelos, sin embargo, Watson y Dallwitz (1992) señalan para el género micropelos alargados tipo "cloridoide". Éstos, son claramente bicelulares y las células tienen paredes delgadas lo que los lleva al colapso. Esto último explica su ausencia en las ilustraciones.

Los estomas están cubiertos por aguijones o por una célula "papiliforme" intercostal (Figs. 2A, 3A–C). Sus células subsidiarias tienen forma triangular o redonda lo que le confiere al estoma las formas rómbica o en domo respectivamente.

Las células "papiliformes" intercostales, presentes en la epidermis, son únicas en el género *Swallenia*. Estas células están en los márgenes de los surcos y cubren parcial o totalmente los estomas como lo señalan también Watson y Dallwitz (1992). Sin embargo, la epidermis no tiene las papilas típicas ni las cantidades características que se observan en las especies de ambientes secos y salinos (Figs. 2A, 3B–C).

Estas células "papiliformes" intercostales, probablemente funcionan de manera similar y sustituyen a las células buliformes y a aquellas de parénquima incoloro que ocurren en el resto de la subtribu, sin que éstas sean homólogas. Por su posición y estructura, las células "papiliformes" posiblemente sirven como canales para la entrada de luz e intervienen en la apertura y cierre de los surcos cuando la lámina está abierta o cerrada respectivamente. Esto último lleva a la planta a controlar la evapotranspiración.

La micromorfología de la lema (Fig. 4A–C) muestra correlación con las características de la lámina foliar. Además de ser pilosa en la base, posee abundantes aguijones y células cortas. También carece de papilas y micropelos, mientras que, en el resto de los géneros de la subtribu Monanthochloinae las papilas están presentes, los aguijones son escasos y los cuerpos de sílice están con menor frecuencia o son escasos. Los cuerpos de sílice no muestran un patrón definido como lo establecen Valdés y Hatch (1991) en su estudio de la lema de las Eragrostídeas.

Todos los géneros de la subtribu Monanthochloinae comparten la presencia de surcos profundos en la cara adaxial de la lámina y el esclerénquima adaxial distribuido en hebras. Sin embargo, llama la atención la separación de *Swallenia* por 16 de los 18 caracteres diagnósticos que se muestran en el Cuadro 2 (células cortas costales en hileras de hasta 15 células de largo, células papiliformes cubriendo los estomas, papilas ausentes, aguijones

abundantes, micropelos ausentes, lámina nodular, surcos abaxiales y adaxiales, esclerénquima copioso distribuido en grandes hebras, células incoloras ausentes, clorénquima continuo entre haces vasculares sucesivos y por la forma de los haces vasculares y de la vaina externa del haz redonda). Esta observación coincide con la opinión de Renvoize (1983) en el sentido de que *Swallenia* presenta algunas anomalías con respecto al patrón anatómico general de la tribu Eragrostideae.

Las características anatómicas de la lámina foliar y la lema no convalidan los criterios de Clayton y Renvoize (1986) y Peterson et al. (1995, 1997) quienes consideran a *Swallenia* como un género integrante de la subtribu Monanthochloinae. Las observaciones del presente trabajo permiten inferir que las afinidades de *Swallenia* son inciertas, no obstante, es claro que este género no está relacionado con *Distichlis, Allolepis, Jouvea, Monanthochlöe, Reederochloa* (del Nuevo Mundo) y *Aeluropus* (del Viejo Mundo), que son los géneros que mejor conforman la subtribu. Las características morfológicas, anatómicas y de ultraestructura sugieren que *Swallenia* debe separarse de la subtribu Monanthochloinae.

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COMPARATIVE FLOWERING PHENOLOGY OF PLANTS IN THE WESTERN MOJAVE DESERT

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Abstract

Above-average precipitation fell on the western Mojave Desert in February and March 1991, which resulted in the flowering of most plant species that spring. This mass germination event occurred despite the almost total lack of rainfall between September and December 1990, a finding inconsistent with previous observations from the Mojave Desert. The 58+ annual species observed on the study site flowered in a sequential manner from early March to mid-June, 1991.

Climatic phenomena were similar the following year, as several winter storms produced large amounts of precipitation in February and March 1992. Consequently, at least 63 annual and 15 perennial plant species bloomed over spring 1992. Like the previous year, plants flowered sequentially from early March to late June. An analysis of flowering dates between years suggests that timing of flowering for these species is highly consistent from year to year. Some phylogenetic biases in flowering dates were evident among some of the locally-dominant taxa. Species in the families Brassicaceae and Boraginaceae flowered in early spring, whereas species in the Fabaceae, Asteraceae, and Polygonaceae, bloomed from mid- to late-spring. However, Polemoniaceous species flowered throughout spring.

The Mojave Desert has a remarkably diverse ephemeral plant flora consisting of over 250 species and varieties (Shreve and Wiggins 1964). As a result, this region has long attracted biologists interested in germination and flowering phenomena of desert plants (Went 1948, 1949; Juhren et al. 1956; Tevis 1958a, b; Beatley 1967, 1969, 1974; Johnson et al. 1978). These studies from various localities in the Mojave Desert have reached similar conclusions as to environmental requirements for successful germination and community-wide flowering phenology.

Germination of Mojave Desert winter annuals may be a straightforward consequence to particular environmental conditions with regards to the quantity and timing of precipitation. In general, it is thought that a minimum of 20–25 mm of rain is required for successful germination of winter annuals (Went 1948; Juhren et al. 1956; Tevis 1958a; Beatley 1967, 1969, 1974). Seasonal timing of precipitation may also be a critical factor, as Beatley (1974) concluded that successful germination of winter annuals in the Mojave Desert is contingent upon a "critical autumn rain."

Another common finding among previous studies is the observation that different plant species flower in a temporal sequence during the spring growing season. Beatley (1974), who extensively studied plants at the Nevada Test Site in the eastern Mojave Desert (Fig. 1), defined this phenomenon as follows: "flowering and fruiting are phenomena of April and May, with the precise time of anthesis, fruiting, and death varying among the species, and with the elevation and the season, but in any case proceeding in an orderly overlapping species sequence once in progress." Tevis (1958b) also noted sequence-like flowering times for plants growing at a Colorado Desert site. The "Colorado Desert" represents a subdivision of the Sonoran Desert biogeographic province located in southeastern California and is bounded by the Mojave Desert, Little San Bernardino Mountains, Peninsula Ranges, and Colorado River (Turner and Brown, 1982; Fig. 1). At another Colorado Desert site, Burk (1982) also documented interspecific variation in flowering phenology among 18 ephemeral species within and between the spring and summer growing seasons. Yet another example comes from the southern Atacama Desert of southern Chile where Vidiella et al. (1999) described the sequential flowering of 25 annual and perennial species during the spring season. Thus although deserts are defined by their scant and unpredictable precipitation, the within-season timing of flowering may be a more predictable occurrence.

In early 1991 and again in 1992 an El Niño/Southern Oscillation (ENSO) event produced large amounts of precipitation across the California deserts. This afforded the author an opportunity to study flowering phenologies of plants found in the western Mojave Desert. Here, I describe the flowering phenologies for the majority of annual and perennial species coexisting on a single site during spring 1991 and 1992. I also show that the temporal sequence of flowering within a single growing season is predictable.

Materials and Methods

This study was conducted at the Desert Tortoise Natural Area (DTNA) in eastern Kern County, California. This 100 km² nature preserve, which is located along the western edge of the Mojave Desert (Fig. 1), contains a variety of vegetation communities including creosote bush scrub, Joshua tree
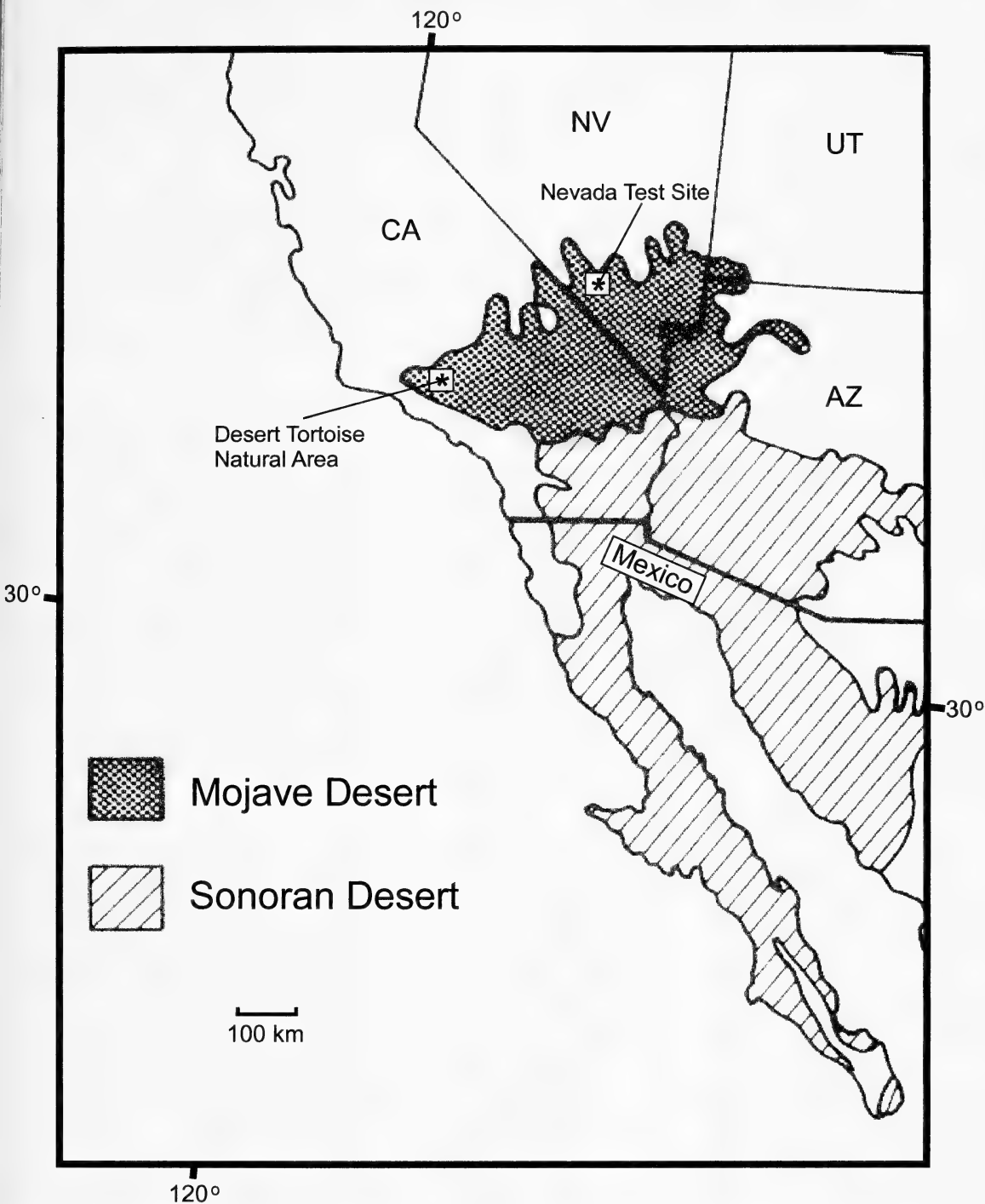
FIG. 1. Map showing the Mojave and Sonoran Deserts in the southwestern United States and adjacent Mexico (after MacMahon, 1988). The locations of the Desert Tortoise Natural Area (Kern County, California) and Nevada Test Site (Nye County, Nevada) are also shown.

woodland, saltbush scrub, and sandy wash. The flora of the DTNA is rich by Mojave Desert standards, as it is comprised of at least 126 annual and 57 perennial species.

Flowering phenologies of annuals and perennials were studied in the northwestern corner of the DTNA (elevation ~900 m) between 1 March–12 June 1991 and 1 March–21 June 1992. Local topography consisted of flat sandy areas interspersed by sandy washes and low rolling, rocky, hills.
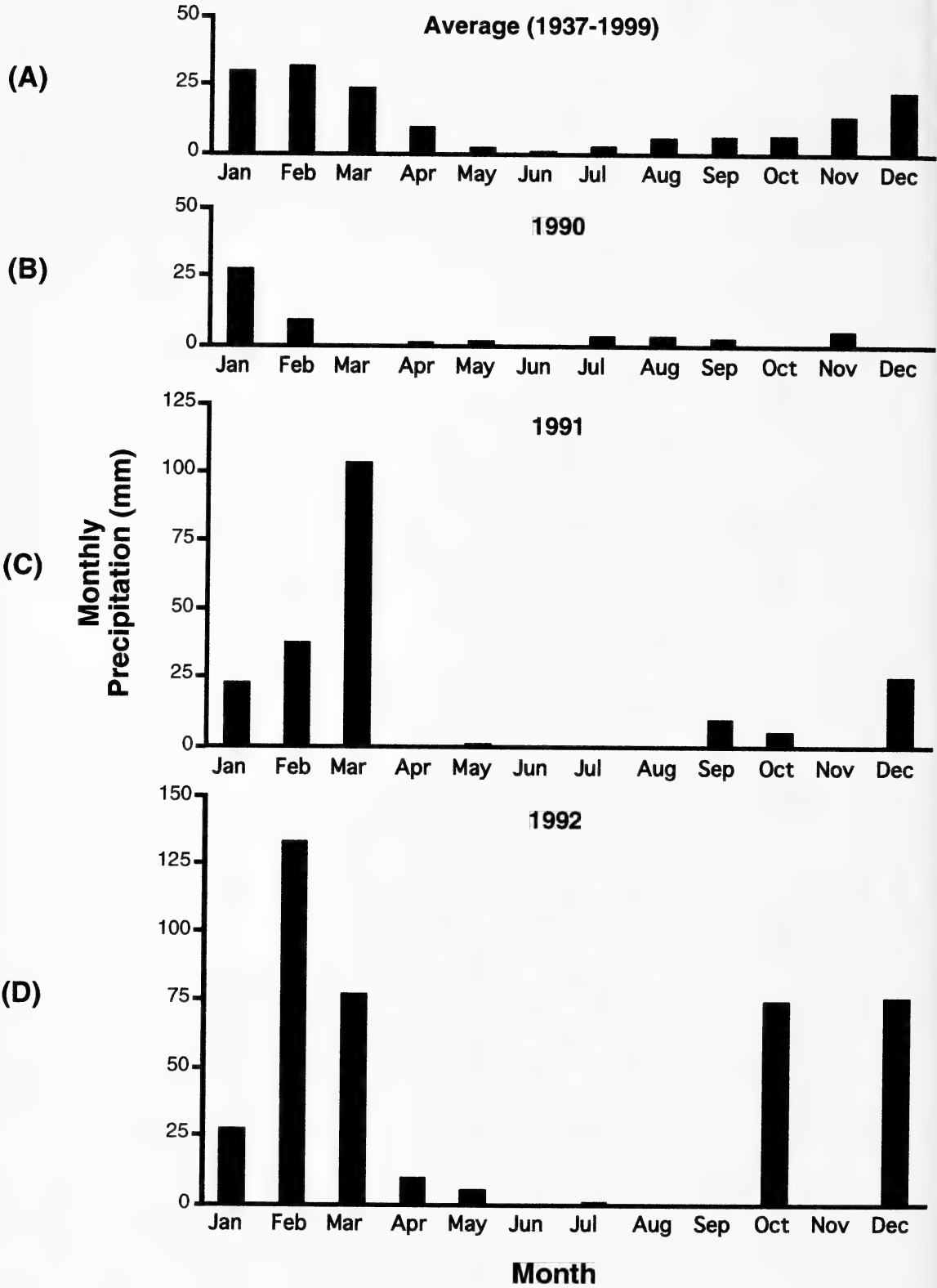
Fig. 2. Monthly precipitation in the western Mojave Desert measured at Randsburg, California 1937–1999: (A) average monthly precipitation for years 1937–1999, (B) total monthly precipitation during 1990, (C) total monthly precipitation during 1991, (D) total monthly precipitation during 1992 (data from NCDC 2000).

SPECIES	FAMILY	MARCH	APRIL	MAY	JUNE
Tropidocarpum gracile	Brassicaceae				
Erodium cicutarium	Geraniaceae				
Gilia minor	Polemoniaceae				
Phacelia fremontii	Hydrophyllaceae				
Lasthenia californica	Asteraceae				
Lepidium flavum	Brassicaceae				
Guillenia lasiophylla	Brassicaceae				
Amsinckia tessellata	Boraginaceae				
Linanthus dichotomus	Polemoniaceae				
Pectocarya spp.	Boraginaceae				
Phacelia tanacetifolia	Hydrophyllaceae				
Coreopsis bigelovii	Asteraceae				
Cryptantha angustifolia	Boraginaceae				
Pholistoma membranaceum	Hydrophyllaceae				
Cryptantha nevadensis	Boraginaceae				
Eschsholzia minutiflora	Papaveraceae				
Mentzelia eremophila	Loasaceae				
Caulanthus inflatus	Brassicaceae				
Oxytheca perfoliata	Polygonaceae				
Chorizanthe watsonii	Polygonaceae				
Chorizanthe brevicornu	Polygonaceae				
Mentzelia spp.	Loasaceae				
Gilia latiflora	Polemoniaceae				
Syntrichopappus fremontii	Asteraceae				
Caulanthus cooperi	Brassicaceae				
Camissonia palmeri	Onagraceae				
Cryptantha pterocarya	Boraginaceae				
Lupinus odoratus	Fabaceae				
Descurainia pinnata	Brassicaceae				
Camissonia campestris	Onagraceae				
Eriogonum pusillum	Polygonaceae				
Salvia columbariae	Lamiaceae				
Plantago ovata	Plantaginaceae				
Salvia carduacea	Lamiaceae				
Chaenactis fremontii	Asteraceae				
Calycoseris parryi	Asteraceae				
Cryptantha circumcissa	Boraginaceae				
Malacothrix glabrata	Asteraceae				
Nama demissum	Hydrophyllaceae				
Lotus humistratus	Fabaceae				
Centrostegia thurberi	Polygonaceae				
Malacothrix coulteri	Asteraceae				
Eriophyllum pringlei	Asteraceae				
Eriogonum gracillimum	Polygonaceae				
Astragalus didymocarpus	Fabaceae				
Linanthus parryae	Polemoniaceae				
Glyptopleura marginata	Asteraceae				
Chaenactis carphoclinia	Asteraceae				
Loeseliastrum schottii	Polemoniaceae				
Eriogonum nidularium	Polygonaceae				
Nemacladus spp.	Campanulaceae				
Langloisia setosissima ssp. *punctata*	Polemoniaceae				
Camissonia boothii	Onagraceae				
Chorizanthe rigida	Polygonaceae				
Prenanthella exigua	Asteraceae				
Eriastrum eremicum	Polemoniaceae				
Eriogonum angulosum	Polygonaceae				
Eremocarpus setigerus	Euphorbiaceae				

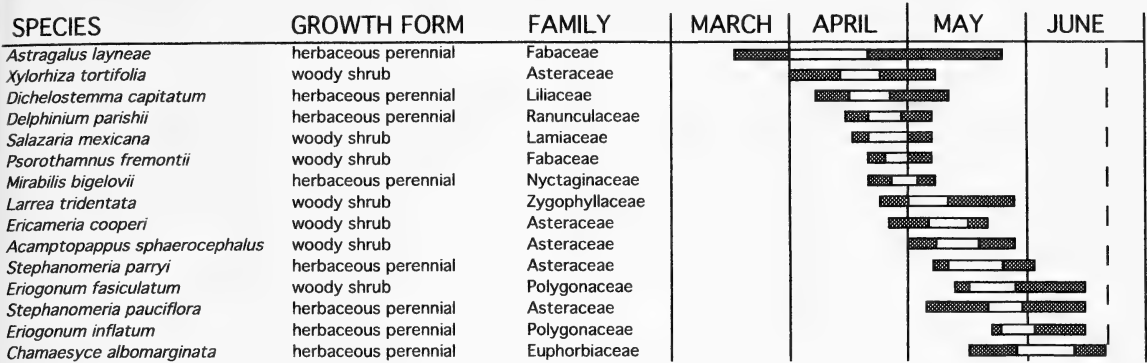Fig. 3. Dates of first flowering for 58+ species of annual plants at the Desert Tortoise Natural Area, eastern Kern County, California during spring 1991.

SPECIES	FAMILY	MARCH	APRIL	MAY	JUNE
Lepidium lasiocarpum	Brassicaceae				
Tropidocarpum gracile	Brassicaceae				
Pholistoma membranaceum	Hydrophyllaceae				
Pectocarya spp.	Boraginaceae				
Erodium cicutarium	Geraniaceae				
Gilia minor	Polemoniaceae				
Cryptantha nevadensis	Boraginaceae				
Guillenia lasiophylla	Brassicaceae				
Cryptantha pterocarya	Boraginaceae				
Mentzelia spp.	Loasaceae				
Amsinckia tessellata	Boraginaceae				
Eschscholzia minutiflora	Papaveraceae				
Lepidium flavum	Brassicaceae				
Lasthenia californica	Asteraceae				
Phacelia tanacetifolia	Hydrophyllaceae				
Phacelia fremontii	Hydrophyllaceae				
Caulanthus inflatus	Brassicaceae				
Caulanthus cooperi	Brassicaceae				
Linanthus dichotomus	Polemoniaceae				
Uropappus lindleyi	Asteraceae				
Astragalus acutirostris	Fabaceae				
Mentzelia eremophila	Loasaceae				
Malacothrix coulteri	Asteraceae				
Descurainia pinnata	Brassicaceae				
Syntrichopappus fremontii	Asteraceae				
Cryptantha circumscissa	Boraginaceae				
Camissonia campestris	Onagraceae				
Coreopsis bigelovii	Asteraceae				
Camissonia palmeri	Onagraceae				
Gilia latiflora	Polemoniaceae				
Linanthus parryae	Polemoniaceae				
Lupinus odoratus	Fabaceae				
Monoptilon bellioides	Asteraceae				
Centrostegia thurberi	Polygonaceae				
Eriogonum pusillum	Polygonaceae				
Astragalus didymocarpus	Fabaceae				
Oxytheca perfoliata	Polygonaceae				
Cryptantha angustifolia	Boraginaceae				
Eriophyllum pringlei	Asteraceae				
Malacothrix glabrata	Asteraceae				
Salvia carduacea	Lamiaceae				
Chaenactis fremontii	Asteraceae				
Nama demissum	Hydrophyllaceae				
Nemacladus spp.	Campanulaceae				
Calycoseris parryi	Asteraceae				
Plantago ovata	Plantaginaceae				
Chorizanthe watsonii	Polygonaceae				
Lotus humistratus	Fabaceae				
Glyptopleura marginata	Asteraceae				
Mucronea perfoliata	Polygonaceae				
Loeseliastrum schottii	Polemoniaceae				
Chaenactis carphoclinia	Asteraceae				
Salvia columbariae	Lamiaceae				
Chorizanthe brevicornu	Polygonaceae				
Eriogonum nidularium	Polygonaceae				
Eriogonum gracillimum	Polygonaceae				
Prenanthella exigua	Asteraceae				
Camissonia boothii	Onagraceae				
Chorizanthe rigida	Polygonaceae				
Eriastrum eremicum	Polemoniaceae				
Langloisia setosissima ssp. *punctata*	Polemoniaceae				
Eriogonum angulosum	Polygonaceae				
Eremocarpus setigerus	Euphorbiaceae				

SPECIES	GROWTH FORM	FAMILY	MARCH	APRIL	MAY	JUNE
Astragalus layneae	herbaceous perennial	Fabaceae				
Xylorhiza tortifolia	woody shrub	Asteraceae				
Dichelostemma capitatum	herbaceous perennial	Liliaceae				
Delphinium parishii	herbaceous perennial	Ranunculaceae				
Salazaria mexicana	woody shrub	Lamiaceae				
Psorothamnus fremontii	woody shrub	Fabaceae				
Mirabilis bigelovii	herbaceous perennial	Nyctaginaceae				
Larrea tridentata	woody shrub	Zygophyllaceae				
Ericameria cooperi	woody shrub	Asteraceae				
Acamptopappus sphaerocephalus	woody shrub	Asteraceae				
Stephanomeria parryi	herbaceous perennial	Asteraceae				
Eriogonum fasiculatum	woody shrub	Polygonaceae				
Stephanomeria pauciflora	herbaceous perennial	Asteraceae				
Eriogonum inflatum	herbaceous perennial	Polygonaceae				
Chamaesyce albomarginata	herbaceous perennial	Euphorbiaceae				

FIG. 5.   Flowering phenologies for 15 species of perennial plants at the Desert Tortoise Natural Area, eastern Kern County, California during spring 1992. Horizontal bars illustrate the flowering phenology of each species as follows: shaded bar to left of white bar = "first flowering" stage, white bar = "peak flowering" stage; and shaded bar to right of white bar = "past-peak flowering" stage. Vertical dashed line shows the final day of observations, June 21, 1992.

Dominant species of shrubs in this area were *Larrea tridentata* (DC.) Cov., *Ambrosia dumosa* (A. Gray) Payne, and *Acamptopappus sphaerocephalus* A. Gray. Daily and monthly precipitation data were obtained from climatic records of Randsburg, California (22 airline km away), a NOAA station since 1937 (National Climatic Data Center [NCDC], 2000).

Observations were generally made several times per week throughout the study period. However, as this study was in a pilot stage during 1991, phenological data for that year only consists of dates of first flowering for each species, whereas the 1992 data set contains additional phenological data (see below) for each species. Field identification of species of *Nemacladus, Pectocarya,* and *Mentzelia* (except for *M. eremophila* (Jepson) H. J. Thompson & Joyce Roberts) proved difficult therefore I only considered these taxa at the level of genus and family in all analyses. Nomenclature follows Hickman (1993). Flowering phenology of each species was subjectively partitioned into four stages: "first flowering": minority of individuals in flower; "peak flowering": most individuals in flower; "past-peak flowering": majority of individuals still succulent but few still in flower; and "dried": majority of individuals in dried state or, in the case of shrubs, are completely in seed.

I analyzed seasonal variation in flowering dates by comparing the 1991 and 1992 first flowering dates for each annual species. Concordance of relative flowering dates would suggest that species' flowering times are predictable.

RESULTS

Following 1990, a period of well-below normal precipitation, winter storms across the western Mojave Desert produced well-above average precipitation during February and March 1991 and again during the same period in 1992 (Fig. 2A–D; NCDC, 2000). Not only were climatic conditions nearly duplicated both years, but the diversity of plants that underwent flowering was also quite similar.

Annuals in 1991 flowered between early March and middle June (Fig. 3). Observations ended in middle June 1991 so it is unknown if any plants bloomed over summer. However, it is doubtful that many could have flowered because few annuals were even succulent in June. An examination of first flowering dates for 58+ annual species in 1991 reveals substantial temporal variation in flowering with some species beginning to flower in early March, while others didn't start blooming until April, May, or even June (Fig. 3).

Complete flowering-phenology data were obtained for 63+ annual and 15 perennial species during spring 1992. Like 1991, much seasonal variation in flowering was apparent, as annuals and perennials apparently flowered in a sequential manner throughout spring (Fig. 4, 5). It remains unknown if any plants bloomed over summer 1992 but, again, few annuals were even green by June so it is doubtful the flowering season extended much further. Most annuals remained in their peak flowering stage for only 1–2 weeks but some main-

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FIG. 4.   Flowering phenologies for 63+ species of annual plants at the Desert Tortoise Natural Area, eastern Kern County, California during spring 1992. Horizontal bars illustrate the flowering phenology of each species as follows: shaded bar to left of white bar = "first flowering" stage, white bar = "peak flowering" stage; and shaded bar to right of white bar = "past-peak flowering" stage. Vertical dashed lines shows the final day of observations, June 21, 1992.

tained this stage for up to a month (Fig. 4). Following the peak flowering stage very few annuals remained in flower beyond a month (Fig. 4). While some annuals began flowering in early March, no perennials bloomed until April (Fig. 5). However, like the annuals the perennials displayed considerable temporal variation in flowering (Fig. 5).

A comparison of first flowering dates for over 58 annual species between 1991 and 1992 indicates that between year flowering dates were remarkably similar (Fig. 6). This suggests that the observed temporal variation in flowering is mostly sequential and predictable. Furthermore, this sequence in flowering times occurred irrespective of growth form, as species of annuals, herbaceous perennials, and woody shrubs flowered throughout spring (Fig. 3–5).

An examination of the phenological sequence from the level of plant family suggests a possible phylogenetic connection, as species within the families Brassicaceae and Boraginaceae bloomed early in the growing season while the Fabaceae, Asteraceae, and Polygonaceae flowered relatively late (Fig. 7). However, not all families displayed seasonal specificity in flowering, as members of the Polemoniaceae flowered throughout spring (Fig. 7).

DISCUSSION

The variable nature of desert rainfall was evident in the western Mojave Desert during the early 1990s. Little rain fell in 1990 while relatively large amounts fell in early 1991 and again in 1992. These substantial rainfall events promoted the flowering of nearly every plant species known from the study site each year. The duration of the flowering season as well as the general flowering sequence of species was also strikingly similar both years.

Beatley (1967, 1969, 1974) hypothesized that successful germination of Mojave Desert winter annuals is contingent upon a >25 mm rainfall event occurring sometime between late September and mid-December. Yet apparently most winter annuals at the DTNA flowered throughout spring 1991 even though almost no rain fell in the area the previous autumn and early winter period. Therefore, germination of DTNA annuals must have occurred in response to ENSO-driven rains falling in early 1991. The first winter storm of 1991 passed through the area between January 3–5 leaving an accumulation of 19 mm of precipitation (Table 1). While some plants may have flowered in response to this minor rainfall event (see Went 1948; Beatley 1974), it seems much more likely that the storm(s) of February 28 through March 5 caused the massive flowering of plants, as over 67 mm of rain fell during this brief period (Table 1). Another series of storms passed through the area between March 19–28 resulting in a total of 73 mm of precipitation (Table 1).

Climatic and flowering phenomena during early 1992 were extraordinarily similar to the same period the year before. The autumn and early winter period of 1991 was very dry with only 22.5 mm of precipitation from five different rainfall events (Table 1). Flowering in early 1992 must have been triggered by the 47.1-mm rainfall event of late December to early January or the 134.5-mm event in early February (Table 1). Two additional storms passed through the area in early and late March leaving accumulations of 23.7 and 64 mm of rain respectively (Table 1).

These results are noteworthy because Beatley (1967, p. 746) noted that native winter annuals at the Nevada Test Site never germinated during the months January–September regardless of rainfall during this period. Why then did native winter annuals in the western Mojave Desert respond to late winter rainfall and in such dramatic fashion? The annual plant floras in the eastern and western regions of the Mojave Desert are roughly similar, especially at the level of family (Beatley 1967, 1974). This raises the possibility that winter annuals in the eastern Mojave Desert have different germination requirements than their relatives in the western Mojave Desert.

Indeed, geographic variation in climate may help explain this paradox. The eastern Mojave Desert experiences substantial rainfall events during summer and autumn (Beatley 1974; Turner 1982). Winter annuals in this region must have restrictive germination requirements otherwise a heavy downpour in the middle of summer could trigger germination, which might be maladaptive for these C_3 annuals (Mulroy and Rundel 1977). On the other hand, winter annuals in the western Mojave Desert are not faced with this problem owing to the lack of summer rainfall (Turner 1982) so more flexible germination requirements may be a more advantageous strategy. Cool and moist conditions during the late winter-spring period of 1991 and 1992 in the western Mojave Desert seemed to be ideal for winter annual growth and reproduction. Perhaps these plants would have "missed out" had they not responded to late winter precipitation. Thus, geographical differences in climate may select for region-specific germination strategies but more research is needed to precisely determine what environmental variables other than rainfall influence germination in these plants.

Sequential flowering of desert plants seems to be a general phenomenon and involving species of various growth forms and phylogenetic lineages (Beatley 1974; Tevis 1958b; Vidiella et al. 1999; this study; also see Poole and Rathcke 1979; Stiles 1979; Cole 1981; Rathcke 1984). While Beatley (1974) suggested that species' flowering times are predictable, to my knowledge there has been no multi-year comparison of flowering dates for any Mojave Desert community to corroborate this hypothesis. In the present study, I have demonstrated that first flowering dates for an winter annual com-
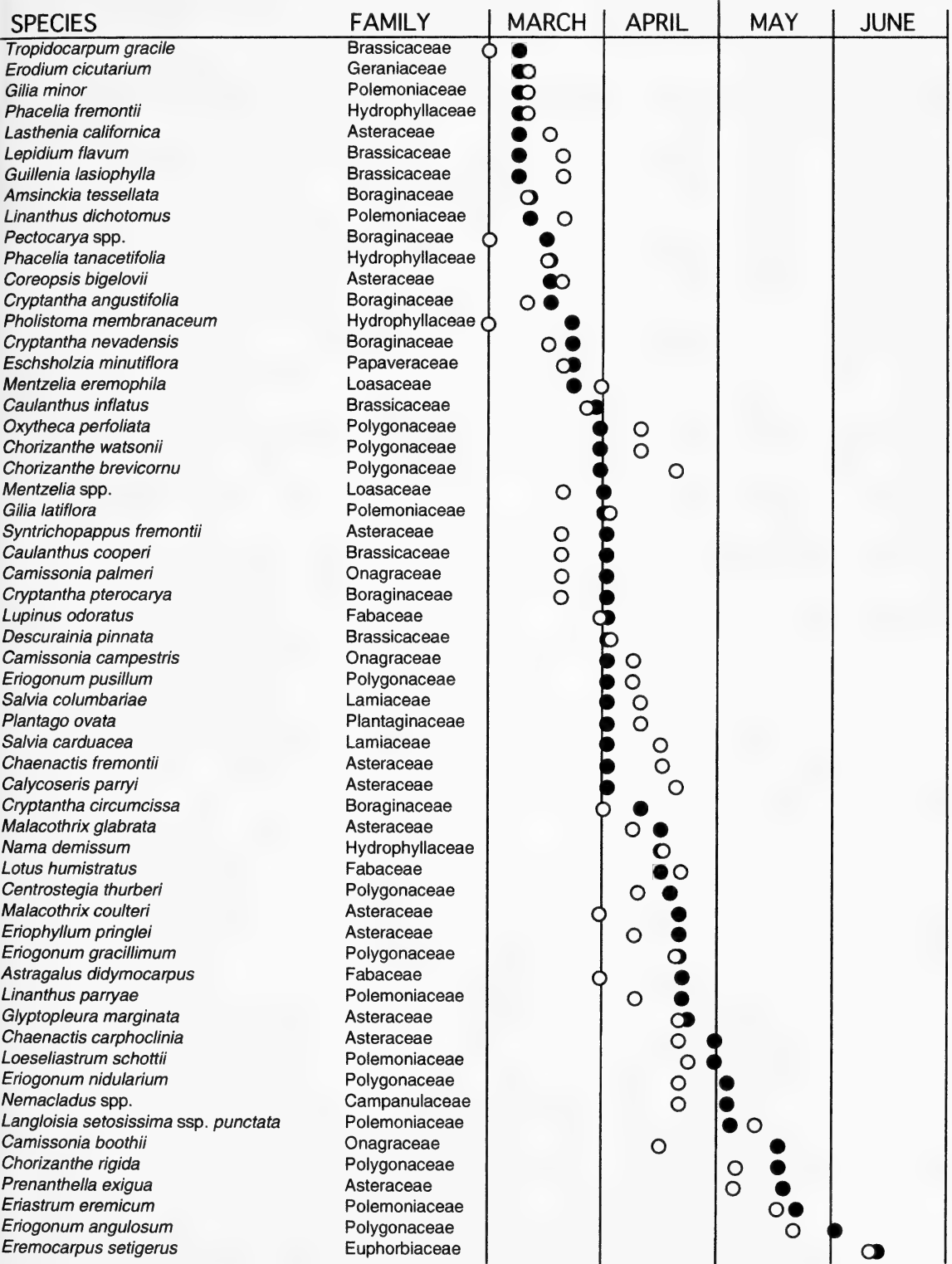
SPECIES	FAMILY	MARCH	APRIL	MAY	JUNE
Tropidocarpum gracile	Brassicaceae				
Erodium cicutarium	Geraniaceae				
Gilia minor	Polemoniaceae				
Phacelia fremontii	Hydrophyllaceae				
Lasthenia californica	Asteraceae				
Lepidium flavum	Brassicaceae				
Guillenia lasiophylla	Brassicaceae				
Amsinckia tessellata	Boraginaceae				
Linanthus dichotomus	Polemoniaceae				
Pectocarya spp.	Boraginaceae				
Phacelia tanacetifolia	Hydrophyllaceae				
Coreopsis bigelovii	Asteraceae				
Cryptantha angustifolia	Boraginaceae				
Pholistoma membranaceum	Hydrophyllaceae				
Cryptantha nevadensis	Boraginaceae				
Eschsholzia minutiflora	Papaveraceae				
Mentzelia eremophila	Loasaceae				
Caulanthus inflatus	Brassicaceae				
Oxytheca perfoliata	Polygonaceae				
Chorizanthe watsonii	Polygonaceae				
Chorizanthe brevicornu	Polygonaceae				
Mentzelia spp.	Loasaceae				
Gilia latiflora	Polemoniaceae				
Syntrichopappus fremontii	Asteraceae				
Caulanthus cooperi	Brassicaceae				
Camissonia palmeri	Onagraceae				
Cryptantha pterocarya	Boraginaceae				
Lupinus odoratus	Fabaceae				
Descurainia pinnata	Brassicaceae				
Camissonia campestris	Onagraceae				
Eriogonum pusillum	Polygonaceae				
Salvia columbariae	Lamiaceae				
Plantago ovata	Plantaginaceae				
Salvia carduacea	Lamiaceae				
Chaenactis fremontii	Asteraceae				
Calycoseris parryi	Asteraceae				
Cryptantha circumcissa	Boraginaceae				
Malacothrix glabrata	Asteraceae				
Nama demissum	Hydrophyllaceae				
Lotus humistratus	Fabaceae				
Centrostegia thurberi	Polygonaceae				
Malacothrix coulteri	Asteraceae				
Eriophyllum pringlei	Asteraceae				
Eriogonum gracillimum	Polygonaceae				
Astragalus didymocarpus	Fabaceae				
Linanthus parryae	Polemoniaceae				
Glyptopleura marginata	Asteraceae				
Chaenactis carphoclinia	Asteraceae				
Loeseliastrum schottii	Polemoniaceae				
Eriogonum nidularium	Polygonaceae				
Nemacladus spp.	Campanulaceae				
Langloisia setosissima ssp. *punctata*	Polemoniaceae				
Camissonia boothii	Onagraceae				
Chorizanthe rigida	Polygonaceae				
Prenanthella exigua	Asteraceae				
Eriastrum eremicum	Polemoniaceae				
Eriogonum angulosum	Polygonaceae				
Eremocarpus setigerus	Euphorbiaceae				

FIG. 6. First flowering dates for 58+ species of annual plants in 1991 (black circles) and 1992 (white circles) at the Desert Tortoise Natural Area, eastern Kern County, California.

FIG. 7. Distribution of peak flowering dates among annuals and perennials within six selected families throughout spring 1992. Horizontal axis represents the particular week when each species entered its "peak-flowering" stage. Vertical axis is the number of species within a given family. Only families with at least six species found at the study site were included.

munity were remarkably consistent between years thereby supporting Beatley's observations.

As to the evolution of species' specific flowering times, this could be driven either by ecological interactions (Mosquin 1971; Stiles 1977; Waser 1978; Gleeson 1981; Rathcke and Lacey 1985) or by phylogenetic relatedness (Vidiella et al. 1999; this study). Previous investigations have largely taken the ecological approach such as looking at the influence of limited pollinator availability (Mosquin 1971; Stiles 1977; Waser 1978; Gleeson 1981; Rathcke and Lacey 1985), while few studies have taken phylogeny into account (but see Kochmer and Handel 1986; Vidiella et al. 1999). This study provides weak evidence that the timing of flowering for some plants may be due to phylogeny rather than solely to ecological factors. Additional research should be undertaken in an effort to elucidate the relative roles of ecology and phylogeny in arranging the temporal aspect of plant community structure.

TABLE 1. RAINFALL EVENTS AT RANDSBURG, CALIFORNIA BETWEEN SEPTEMBER 1990 AND JUNE 1992. RAINFALL ON CONSECUTIVE DAYS OR WITHIN A 3-DAY PERIOD IS CONSIDERED A SINGLE RAINFALL EVENT (DATA FROM NCDC 2000).

	Rainfall (mm)
September 20, 1990	2.5
November 19, 1990	5.3
December 20, 1990	0.3
January 3–5, 1991	19.0
January 10, 1991	4.5
February 17, 1991	1.8
February 28–March 5, 1991	67.0
March 14, 1991	1.0
March 19–28, 1991	73.1
May 21, 1991	1.0
September 5, 1991	6.0
September 22, 1991	3.8
October 26, 1991	5.3
November 14, 1991	0.5
December 8–11, 1991	7.0
December 28–January 8, 1992	47.1
February 6–16, 1992	134.5
March 1–7, 1992	23.8
March 21–April 2, 1992	64.8
May 7, 1992	5.8

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SURVEY OF *JUNIPERUS COMMUNIS* (CUPRESSACEAE) L. VARIETIES FROM THE WESTERN UNITED STATES USING RAPD FINGERPRINTS

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ABSTRACT

RAPD fingerprints were generated from seven wild populations of *Juniperus communis* L. to assess whether molecular data support subdivision into vars. *saxatilis, jackii* and *sibirica,* members of California Floristic Province, and *depressa,* a component of the Great Basin Floristic Province. Results from UPGMA and Neighbor Joining cluster analyses showed little correspondence between RAPD-derived distances and varietal boundaries. *Juniperus communis* var. *jackii,* in particular, was highly heterogeneous, lending support to the hypothesis that the characteristic growth habit of this serpentine dweller (elongated, sparsely branched lateral branches) is environmentally induced. In contrast to the RAPD results, nucleotide sequences of the ITS1 region of nuclear ribosomal DNA were identical in four of five var. *jackii* individuals sequenced, and the fifth exhibited three base substitutions.

Juniperus communis L. is a circumboreal species of juniper (Franco 1962) characterized by acicular leaves. Two varieties of *J. communis* (Cronquist et al. 1972; Adams 1993) are encountered in the western United States. *Juniperus communis* var. *depressa* Pursh is native to the Great Basin Floristic Province, extends northward into Alaska and eastward across much of Canada and the Great Lakes region, arching south along the east coast to North Carolina. *Juniperus communis* var. *saxatilis* Pallas occurs from British Columbia southward into California in the Cascade Ranges, North Coast Ranges, and Sierra Nevada, but also has a circumboreal distribution outside North America (Adams 1993).

The two varieties differ primarily in habit, leaf size and shape and width of the glaucous stomatal band on the adaxial leaf surface. Although both are low-growing, variety *depressa* develops a somewhat erect main stem whereas variety *saxatilis* is entirely prostrate. Leaf dimensions are ca. 1.0–1.6 mm broad × (6) 10–18 mm long (*depressa*) and (1.2) 1.5–1.8 mm broad × 5–10 (12) mm long (*saxatilis*) (Cronquist et al. 1972), and the glaucous stomatal band is as broad as, or narrower, than each green margin (*depressa*) or 2–3 times as broad as each green margin (*saxatilis*; Franco 1962).

In California, two other varieties are occasionally distinguished. *Juniperus communis* var. *jackii* Rehder (Rehder 1940) differs from var. *saxatilis* by having longer, more sparsely branched lateral branches and is encountered on serpentinite substrates of inland coastal areas in northern California and Oregon. *Juniperus communis* var. *sibirica* Rydb. is described as a very prostrate, almost mat-like, form found on coastal bluffs and in the ex-

treme northwest of California and southwestern Oregon, and as a disjunct population at Ebbett's Pass in the Sierra Nevada. According to Roof (1973), this variety is characterized by leaves that are more incurved, making it less prickly to the touch than *J. communis* vars. *jackii* or *saxatilis.* Adams (1993) and Cronquist et al. (1972) placed varieties *jackii* and *sibirica* in synonymy under *J. communis* var. *montana,* a name recently placed in synonymy under var. *saxatilis* (Farjon 1998). Our previous paper (Ashworth et al. 1999) used the older varietal epithet.

The purpose of this study was to make a preliminary assessment of genetic variability among the four varieties of *J. communis* in the Western United States and to examine whether molecular data favors one of the taxonomic schemes over another. Specifically, do the data support a subdivision into vars. *depressa* and *saxatilis,* and/or is there evidence supporting the recognition of varieties *sibirica* and *jackii*? A second goal was to ascertain whether the mats formed by these creeping junipers are genetically uniform (i.e., clonal) or harbor distinct genotypes. RAPD analysis was chosen as a quick and relatively inexpensive means of getting a fingerprint of the genome of plants from each of the native populations. This technique has been applied successfully to interspecific studies in *Juniperus* (Adams and Demeke 1993). Additionally, sequences of the ITS1 spacer region of the nuclear ribosomal DNA were generated for a subset of seven samples.

METHODS

Plant material. Plant material was gathered from seven wild *Juniperus communis* populations representing vars. *saxatilis* (*sa*A–*sa*C, *sa*G) and *depressa* (*de*D–*de*F). Under the alternative taxonomic scheme, populations *sa*A and *sa*G correspond to *J.*

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TABLE 1. COLLECTION LOCALITIES AND ALTERNATIVE VARIETAL DELIMITATIONS, WITH *JUNIPERUS COMMUNIS* SEGREGATED INTO TWO VARIETIES (*DEPRESSA* AND *SAXATILIS*, AS IN FLORA OF NORTH AMERICA COMMITTEE (1993) AND CRONQUIST ET AL. (1972); A) OR FOUR VARIETIES (*DEPRESSA* AND *SAXATILIS*, AS WELL AS *JACKII SENSU* REHDER AND "*SIBIRICA*" *SENSU* RYDBERG; B).

Sample designation	Varietal delimitation A	Varietal delimitation B	Collection locality
*sa*A1–*sa*A7	*saxatilis*	*sibirica*	OR, Curry County: Cape Sebastian
*sa*B1–*sa*B6	*saxatilis*	*jackii*	CA, Del Norte County: Gasquet Toll Road; two sites ca. 1 mile apart
*sa*C1–*sa*C2	*saxatilis*	*jackii*	CA, Humboldt County: Onion Mountain/Onion Lake intersection
*sa*G1–*sa*G3	*saxatilis*	*sibirica*	CA, Alpine County: Ebbett's Pass, Sierra Nevada
CV2	*saxatilis*	*saxatilis*	OR, Hood River County, Mt. Hood
CV5	*saxatilis*	*sibirica*	OR, Curry County, 'Gold Beach'
CV11	*saxatilis*	*sibirica*	CA, Del Norte County, 'Point St. George'
*de*D	*depressa*	*depressa*	UT, Iron County: between Cedar Breaks National Monument and Pan guitch
*de*E	*depressa*	*depressa*	UT, Iron County: Cedar Breaks National Monument
*de*F	*depressa*	*depressa*	NV, White Pine County: Wheeler Mtn., Great Basin National Park

communis var. *sibirica* and populations *sa*B and *sa*C to *J. communis* var. *jackii*. Table 1 summarizes collection details and taxonomic designations of each of the native populations (see Ashworth et al. 1999 for more complete information), as well as for three cultivated accessions originating from Mount Hood, OR (CV2), Gold Beach, OR (CV5), and Point St. George, CA (CV11), that were included in this study. These three plants grow at Rancho Santa Ana Botanic Garden but were established from cuttings collected in the wild. In a previous study that included both native and non-native *Juniperus* species (Ashworth et al. 1999) they clustered with the native *J. communis* varieties. CV2 represents *J. communis* var. *saxatilis* under all taxonomic systems presented here. CV5 and CV11 are var. *saxatilis* sensu Adams (1993) and Cronquist et al. (1972) and var. *sibirica* sensu Rydberg.

DNA analysis. Information on DNA extraction method, PCR reaction conditions and RAPD primer sequences are detailed in Ashworth et al. 1999. Bands were scored as present or absent by the first and last author. Average taxonomic distances generated from these binary scores were analyzed using the clustering algorithm UPGMA (Unweighted pair group method with arithmetic averages; Sneath and Sokal 1973) and Neighbor-Joining (NJ; Saitou and Nei 1987) available on PAUP* version 4.0 β1 (Swofford 1998). Effects of alternative measures of distance/similarity on clustering were explored using NTSYS version 2.0 (Rohlf 1993). Jaccard coefficients of similarity were calculated using the NTSYS 'SIMQUAL' module, and the cophenetic correlation coefficient was determined via the COPH and MXCOMP modules.

Sequences of the ITS1 spacer region were generated using the forward primer ITS5 (GGAAG-TAAAAGTCGTAACAAGG) and reverse primer ITS4 (TCCTCCGCTTATTGATATGC; both primers from White et al. 1990). Amplification conditions consisted of 40 cycles, each with three suc-

cessive phases of (1) 97°C for 1 min, (2) 48°C for 1 min, and (3) 72°C for 2 min, followed by a final extension time of 7 min at 72°C. Double-stranded template was purified by precipitation in polyethylene glycol/2.5 M NaCl (Morgan and Soltis 1993; Johnson and Soltis 1995) with a 70% and 95% EtOH wash. Single-stranded DNA template was generated by cycle sequencing with incorporation of dye terminators (PRISM™ Dye Terminator Cycle Sequencing Kit with AmpliTaq®; Perkin-Elmer, CT). Settings were 25 cycles of 0.5 min at 95°C, 0.25 min at 50°C and 1 min at 60°C. The resulting product was purified by ethanol precipitation (Sambrook et al. 1989) and electrophoresed on a 6% polyacrylamide gel (Sequagel®) in an Applied Biosystems Model 373A Automated Sequencer. Sequences were proofed and assembled using Sequencher 3.0 (Gene Codes Corporation, Inc., Ann Arbor, MI).

RESULTS

Of 65 primers screened for RAPD analysis, five primers showing scorable and reproducible banding patterns were entered into the final analysis. Scorable bands per primer ranged from one (UBC-329) to nine (UBC-244), with a total of 27 bands scored for 24 individuals. Identical banding patterns were found for *sa*A1, *sa*A3 and *sa*A4, with *sa*A2 differing by a single band.

Figure 1 shows the UPGMA and NJ phenograms generated from distance matrices derived from the RAPD scores. The UPGMA phenogram reveals six main clusters (#1–6), ranging in average within-cluster distance from 0.065 (cluster 4) to 0.273 (cluster 2). CV2 is the most distant accession. Clusters 6 and 5 are linked at a distance of 0.244, with cluster 4 attaching next (0.319), then cluster 3 (0.357), cluster 2 (0.370) and cluster 1 (0.395). Cluster 6 comprises mostly var. *sibirica* (*sa*A1–4, plus CV5, CV11) but also *sa*B4, cluster 5 includes the remaining two members of population *sa*A
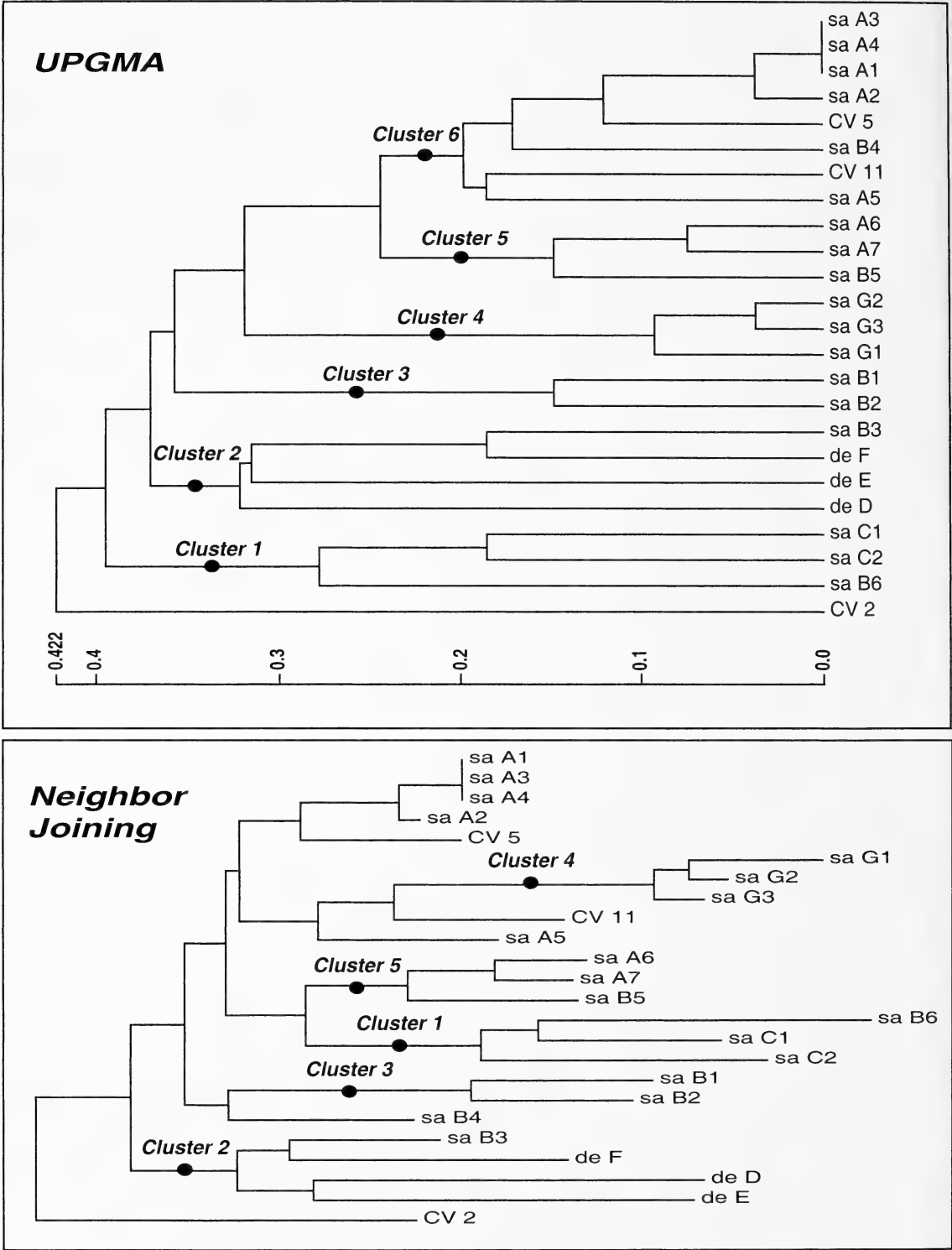
FIG. 1. UPGMA and Neighbor Joining phenograms generated from distances derived from RAPD data of 24 *Juniperus communis* accessions from the western United States.

(*sa*A6, *sa*A7) and also *sa*B5. Cluster 4 comprises population *sa*G, the Sierra Nevadan representatives of var. *sibirica*. Members of population *sa*B (var. *jackii*) appear in five of six clusters, including cluster 2 (*sa*B3) which contains all three accessions of var. *depressa*. Only clusters 1 and 3 contain exclusively var. *jackii*.

UPGMA clustering based on Jaccard coefficients of similarity resulted in identical cluster composition but an altered cluster hierarchy: cluster 3 is the most distant (0.36), followed in order of increasing similarity by CV2, cluster 4, cluster 1, cluster 2, cluster 5 and cluster 6. The matrix correlation coefficient indicates a good fit of distances derived from the phenogram to the original distance matrix.

Five of six clusters present in the UPGMA phenograms are also identified by the NJ algorithm. Three main differences emerge from a comparison of the UPGMA and NJ phenograms: (1) *sa*B4 resides in cluster 6 (predominantly var. *sibirica*) in the UPGMA tree but near cluster 3 (var. *jackii)* in the NJ tree; (2) population *sa*G, which forms a separate cluster below the bifurcation of clusters 5 and 6 in the UPGMA tree, inserts within cluster 6 in the NJ tree; and (3) clusters 1 and 5 are closest to each other in NJ but placed most distantly in the UPGMA analysis.

Of the seven ITS 1 sequences, identical sequences were found for *sa*B1, *sa*B3–5, and *sa*G1. Only CV2 and *sa*B6 each exhibited three autapomorphic base substitutions, and CV2 additionally had an insertion of three nucleotides.

DISCUSSION AND CONCLUSION

Regardless of the clustering algorithm or distance measure used, our RAPD fingerprint data are unable to clarify relationships among the four *J. communis* varieties *depressa, jackii, saxatilis* or *sibirica.* This is a consequence primarily of the markedly heterogeneous population *sa*B (*saxatilis/jackii*), which suggests that the *jackii* morphology (sparsely branched, elongated branches) is an environmentally induced growth form. Our data thus support Adams (1993) and Cronquist et al. (1972) who place the variety in synonymy under var. *saxatilis* on the grounds that the *jackii* habit disappears under common garden conditions (p. 15, Adams (1993)). Kruckeberg (1967) cites *J. communis* as an example of a substrate-indifferent ("bodenvag" *sensu* Unger 1836) serpentine dweller but makes no mention of morphological differences between serpentine and non-serpentine plants. It is well documented that the serpentine environment has a major impact on plant growth and adaptation, although the soil substrate is no longer seen as the only factor responsible. Instead, indirect effects, such as greater light availability, also exert a strong selective force (Baskin and Baskin 1988; Gankin and Major 1964). The elongated, sparsely branched habit of var. *jackii* may thus be the result of reduced competition from other vegetation and plentiful light.

The integrity of var. *saxatilis* is contradicted by the fact that the *saxatilis* accessions in this study are never united in a single cluster distinct from var. *depressa.* The proximity of clusters 4, 5 and 6 in the UPGMA analysis lends some support to var. *sibirica,* although this is weakened by the presence of *sa*B4 and *sa*B5. In the NJ analysis cluster 5, with its two *sibirica* representatives *sa*A6 and *sa*A7, is more similar to non-*sibirica* cluster 1 than to the other *sibirica* accessions.

Interestingly, the NJ analysis causes population G to cluster with *sibirica* representatives, consistent with its *sibirica*-like growth habit and in contrast to its geographic origin (Sierra Nevada). Although geographically close to the Great Basin variety *depressa,* none of the analyses presented here show a close association between var. *depressa* and population *sa*G.

Nucleotide substitutions and an insertion in the ITS1 region were revealed only in *sa*B6 and CV2, corroborating their basal placement on the UPGMA phenogram. By contrast, *sa*G1 and four members of the heterogeneous *sa*B population (*sa*B1 and *sa*B2–4) exhibited identical sequences, showing a lack of concordance between RAPD-derived distances and ITS1 sequence divergence.

The absence of support from our RAPD data for a distinction between vars. *saxatilis* and *depressa* is surprising but may be a function of relatively few markers in relation to the number of genotypes studied. A higher marker to genotype ratio and a greater sampling density might clarify some of the variation encountered.

Although our data are unable to provide answers to our taxonomic questions, they nonetheless give insight into the genetic composition of juniper mats. Individuals of var. *saxatilis* population A originated from various positions around the periphery of a large mat. The identical fingerprints of individuals *sa*A1, *sa*A3 and *sa*A4 suggest that this part of the mat is clonal (*sa*A2 differs only by a single band), but individuals *sa*A5–*sa*A7 have distinct fingerprints. This mat is therefore a combination of clonally-spread and seed-derived individuals. Population B was collected from two nearby mats. This makes the great diversity of distinct fingerprints even more surprising and we speculate whether individuals from this population constitute a hybrid swarm.

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CONIFER TREE DISTRIBUTIONS IN SOUTHERN CALIFORNIA

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Abstract

Maps and text describe current distributions of 19 conifer tree species in southern California. Distributions are related to climate, geology, terrain, and other aspects of the environment. Corrections to earlier published descriptions and maps are highlighted. Although species are discussed as components of six vegetation types (closed-cone conifer forest, foothill woodland, mixed evergreen forest, pinyon-juniper woodland, mixed-conifer forest, and subalpine forest), the distribution maps are for species, not vegetation. Species limits correspond to a density as low as 1 tree of the species of concern per 10 ha. Some changes in distribution over the past century, primarily due to fire, can best be interpreted and understood when a species is placed correctly in one of three models: shifting populations, standing populations, and patch mosaic populations.

Because of their value for lumber and fuelwood, the distribution of coniferous trees in southern California has been described since Europeans first settled the region in the late 18th century (Minnich 1988; Minnich and Franco-Vizcaíno 1998). Early accounts include descriptions in Spanish diaries, the Pacific Railroad Survey of the 1850s, the US–Mexico Boundary survey of 1894, early explorers, and reports of the U.S. Forest Service. The first maps published over 100 years ago by Kinney, Grinnell, and in Forest Reserve Reports were impressionistic or based on life zone theory (Minnich 1988). While forest distributions were realistic, boundary criteria were not explicitly defined. The first objective maps were produced by the Vegetation Type Map Survey (VTM) in 1929–34 (Colwell 1988) on the basis of physiognomy and dominance criteria. Map accuracy was compromised because boundaries were drawn in the field without the advantage of aerial photographs, and their precision was reduced by planometric error of triangulated 1900 topographic base maps. Still, the VTM maps show high quality and are consistent with the earliest aerial photographs in 1928–1939. Griffin and Critchfield (1976) reproduced the ranges of California trees based largely on maps of the VTM survey.

The population size and extent of species of course are dynamic, so it is essential to update maps to ascertain the impacts of natural disturbances and land management. Using aerial photographs, this study produces maps of coniferous trees in southern California south of lat. 35° and west of the Mojave and Colorado Deserts. In southern California's mediterranean climate, wildland fire is strongly integrated into the ecological function of conifer species. Because conifers are largely nonsprouters, stand-replacement fires have produced important changes in species ranges since the VTM survey. The objectives of this study are to produce a modern baseline of distributions for comparison with the VTM survey, to correct taxonomic errors of the VTM survey, describe species ranges in relation to climate, geology, terrain, and other aspects of the environment, and to evaluate species changes over the 20th century.

Among the various reasons for conducting the VTM Survey, Wieslander (1935) stated that it was important to produce a baseline of vegetation for purposes of replication at some time in the future. Likewise, the hope of this survey of southern California conifer forests is to encourage resurveys to evaluate their broad-scale dynamics over long time scales.

Coastal Southern California. Most conifers grow in the Transverse and Peninsular Ranges that divide the Mojave and Sonoran Deserts from the coastal plains and valleys (Fig. 1). The Transverse Ranges extend from Point Conception to Joshua Tree National Park. The Santa Ynez Mountains join the San Rafael and Sierra Madre Mountains of the South Coast Range of central California. From this junction, a series of parallel ridges that include the Ortega, Santa Paula, and Topatopa Mountains, and Pine Mountain Ridge merge into a single chain that includes the Liebre, San Gabriel, and San Bernardino Mountains, and the plateau of Joshua Tree National Park (place names are located in Table 1). The Tehachapi Mountains of the Sierra Nevada terminate at the Lockwood Valley plateau that contains isolated undissected ranges, including Frazier Mountain, Alamo Mountain, and Mt. Pinos. The plateau is bordered on the north by the San Emigdio Mountains. The north-south Peninsular Ranges include the San Jacinto Mountains that extend from San Gorgonio Pass to the Santa Rosa Mountains. To the west is a series of coastal ranges including the Santa Ana, Palomar, Volcan, Cuyamaca, and Laguna Mountains. Elevations in Transverse Ranges frequently exceed 2000 m, and reach 3080 m at Mt. San Antonio and 3499 m at Mt. San Gorgonio. The more subdued Peninsular Ranges are typically 1000–1800 m, although summit altitudes reach 3273 m at Mt. San Jacinto.

TABLE 1. LOCATION OF PLACE NAMES USED IN TEXT.

Place name	Latitude (°N)		Longitude (°W)	
Aguanga	33	27	116	52
Alamo Mountain	34	40	118	56
Azusa	34	09	117	55
Banner Canyon	33	05	116	33
Barton Flats	34	10	116	53
Bautista Canyon	33	40	116	47
Beechers Bay, Santa Rosa Island	33	59	120	10
Big Bear	34	15	116	56
Big Pine Mountain	34	42	119	39
Big Tujunga Canyon	34	20	118	05
Bluff Lake	34	13	116	58
Butler Peak	34	16	117	00
Cattle Canyon	34	15	117	41
Cerro Nordeste	34	50	119	13
City Creek	34	07	117	10
Cobblestone Mountain	34	36	118	52
Coxcomb Mountains	34	02	115	20
Crestline	34	15	117	15
Cucamonga Peak	34	14	117	35
Cuddy Valley	34	50	119	02
Cuyama River	34	45	119	20
Deep Creek	34	18	117	07
Doone Vallye	33	20	116	55
Eagle Mountains	33	49	115	40
Figueroa Mountain	34	45	119	57
Frazier Mountain	34	47	118	59
Garner Valley	33	37	117	40
Gavilon Hills	33	48	117	20
Government Peak	34	09	117	05
Grapevine Canyon	34	23	117	04
Guatay	32	51	116	34
Gypsum Canyon	33	50	117	43
Hagador Canyon	33	48	117	37
Hesperia	34	24	117	20
Holcomb Creek	34	18	117	00
Holcomb Valley	34	19	116	55
Hurricane Ridge	34	46	119	47
Icehouse Canyon	34	15	117	40
Idyllwild	33	45	116	43
Japacha Peak	32	56	116	43
Keller Peak	34	12	117	03
La Brea Creek	34	57	119	58
Lake Arrowhead	34	15	117	11
Lake Hemet	33	40	116	42
Lake Mathews	33	51	117	26
Lake Piru	34	29	118	45
Lakeview Mountains	33	46	117	04
Lazaro Canyon	34	49	119	50
La Rumerosa	32	30	116	03
Lockwood Valley	34	45	119	02
Los Pinos Mountain	32	46	116	36
Lytle Creek	34	14	117	27
Manzanita Creek	34	47	119	54
McCain Valley	32	45	116	20
Mill Creek	34	05	116	56
Mt. Baden-Powell	34	22	117	46
Mt. Grinnell	34	07	116	49
Mt. Laguna	32	52	116	25
Mt. San Antonio	34	17	117	39
Mt. Waterman	34	21	117	56
Mt. Wilson	34	13	118	04
Ojai	34	27	119	15
Ontario Peak	34	14	117	38
Onyx Summit	34	11	116	43
Ortega Hill	34	34	119	23

TABLE 1.   CONTINUED.

Place name	Latitude (°N)		Longitude (°W)	
Otay Mountain	32	35	116	52
Palmdale	34	35	118	05
Palm Divide	33	42	116	39
Perris	33	48	117	14
Phelan	34	26	117	34
Pinyon Ridge	33	11	116	26
Pinyon Flat	33	37	116	27
Pine Valley	32	50	116	31
Pleasants Peak	33	47	117	38
Pleasant View Ridge	34	25	117	55
Plunge Creek	34	09	117	09
Prairie Fork	34	20	117	42
Purisima Hills	34	44	120	27
Rabbit Peak	33	26	116	14
Raywood Flat	34	03	116	50
Redlands	34	03	117	11
Riverside-Perris Plain	33	50	117	15
Rock Creek	34	25	117	50
Running Springs	34	13	117	06
San Bernardino Ridge	34	08	116	54
San Emigdio Mountains	34	50	119	00
San Gorgonio Mountain	34	06	116	50
San Rafael Mountain	34	43	119	48
Santa Paula Peak	34	26	119	00
Santa Susana Mountains	34	20	118	35
Sawmill Mountain	34	42	118	34
Sespe Creek	35	37	119	22
Sisquoc River	34	51	119	50
Soledad Canyon	34	27	118	18
Sugarloaf Mountain	34	12	116	51
Sulphur Spring Canyon	34	45	119	53
Tahquitz Peak	33	45	116	40
Tecate Peak	32	35	116	43
Temescale Canyon	33	46	117	30
Thomas Mountain	33	38	116	42
Throop Peak	34	21	117	48
Tip Top Mountain	34	15	116	42
Topatopa Mountains	34	32	119	00
Torrey Pines State Beach	32	57	117	16
Vandeventer Flat	33	33	116	33
Warm Springs Mountain	34	36	118	35
Waterman Canyon	34	12	117	17
Whale Peak	33	02	116	18
Wright Mountain	34	20	117	39
Wrightwood	34	21	117	39
Zaca Ridge	34	46	120	01

The climate is mediterranean with winter precipitation and summer drought. Mean winter temperatures range from 10°C in the coastal and desert areas to 0°C at 2500 m in the mountains. Mean temperatures in summer range from 38°C in the desert to 15°C at 2500 m. A shallow marine layer results in mean temperatures of 18–22°C at the coast increasing to 27°C in inland valleys.

Large differences in local conifer species zonation result from strong gradients in average annual precipitation (AAP, Fig. 2). Most precipitation occurs during cold fronts arriving from the North Pacific Ocean. Because winds aloft are southwest to southerly (Minnich 1984), physiographic lift is strongest on the south front of the Transverse Ranges, with the highest AAP in coastal escarpments of the "upwind" Topatopa, San Gabriel, and San Bernardino Mountains (AAP, 90–110 cm). Amounts decrease toward downwind ranges and watersheds—regardless of altitude—due to depletion of storm air mass moisture and descending airflow in rain shadows, including the San Rafael Mountains, Pine Mountain Ridge, Big Bear, and upper Santa Ana River (AAP, 60–80 cm). Farther inland, the San Emigdio, Tehachapi, and Liebre Mountains, Mt. Pinos, and lee slopes near Big Bear receive only 35–60 cm AAP. The AAP is only 40–60 cm in the Peninsular Ranges because slopes parallel
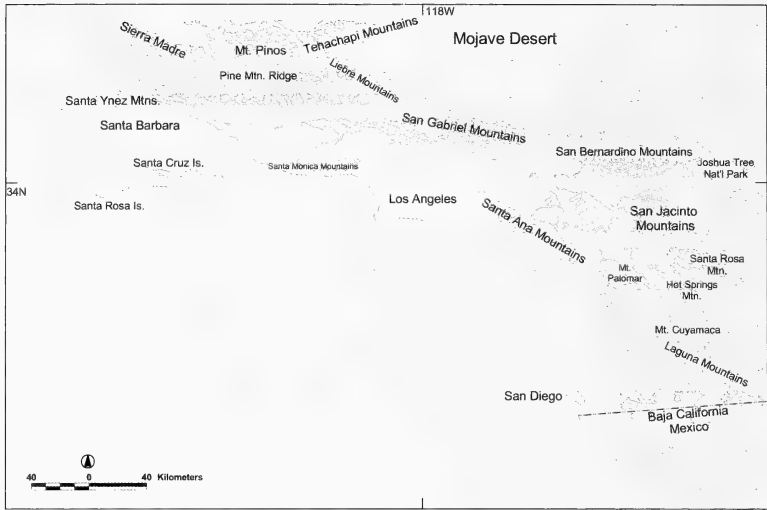
Fig. 1. Location map and place names in southern California. Topographic maps and elevations were developed from United States Geological Survey 1:250,000 Digital Elevation Models (USGS 2000).

storm winds. Amounts locally reach 80–100 cm on local southern escarpments of the Santa Ana Mountains, Mt. Palomar, and Cuyamaca Peak. The San Jacinto Mountains receive 40–70 cm and the Santa Rosa Mountains receive <50 cm because they are leeward of the Santa Ana and Palomar Mountains. The AAP decreases to 10–20 cm in the Mojave and Sonoran Deserts.

METHODS

The large size and distinct morphology of conifers permits accurate mapping to species level using aerial photographs. Maps were interpreted from aerial photographs using a roll film stereoscope (on file in the Department of Earth Sciences, University of California, Riverside). Trees were identified on the basis of their crown perimeter and apex configurations, vertical structure, shadows, and color. We field verified for tree occurrence in all southern California ranges. Procedures are summarized in Minnich (1987a) where maps of many of the same species in northern Baja California were presented.

Distributions were interpreted from a variety of aerial photograph coverages of the entire region taken mostly between 1971–1980 including the Mission 164 coverages of California and photographs taken in 1938–1939. Site-specific georeferencing of repeat aerial photographs on a Zoom Transfer Scope (ZTS) reveals that virtually the same mature trees can be matched on the earliest
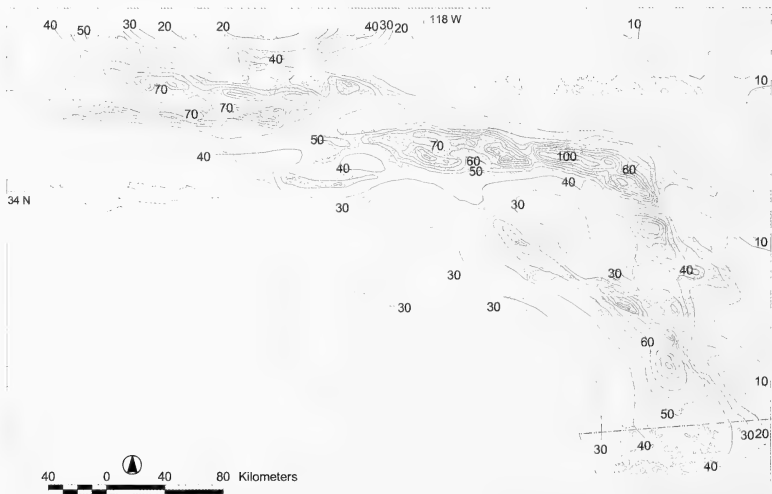
Fig. 2. Mean annual precipitation (after California 1980).
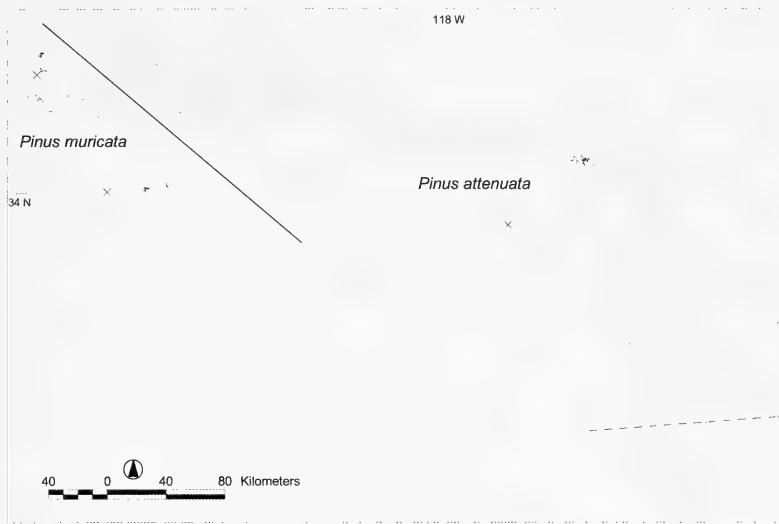
FIG. 3. The distribution of *Pinus attenuata* and *P. muricata*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

and most recent photograph coverages. However, rapid changes occurred in all species from stand-replacement burns. Recent flights (>1990) were examined for stand-replacement burns to update conifer species distributions since the Mission 164 flights.

Since the objective is to map broad species ranges, rather than forest dominance patterns, we defined the limit of species as a minimum threshold of one tree per 10 ha. This criterion allows for more detailed range maps than depicted from Griffin and Critchfield's definition of "group of stands more than two miles (3 km) across, or stands less than two miles (3 km) across or of unknown size." It also excludes rare outposts that would result in excessive detail. Botanical collections are included for the occurrence of outposts outside our species ranges.

Boundary data were georeferenced and transferred onto 1:250,000 scale topographic sheets (USGS 2000) using a ZTS. Contour creation using DTED Level 0 data (NIMA 2001) and subsequent spatial manipulations were performed by Geographical Information Systems using ESRI (2000) software. Graphic versions of the species maps are accessible from our website (http://spotfire/ucr.edu/socaltree). Changes in forest distributions can be evaluated by comparing website maps with published and unpublished VTM quadrangle maps under curation at the University of California, Santa Barbara.

DISTRIBUTIONS

Conifer tree ranges are presented under six vegetation types, as recognized in Barbour and Major (1988): closed-cone conifer forest, foothill woodland, mixed evergreen forest, pinyon-juniper woodland, mixed-conifer forest, and subalpine forest. Species ranges are given from northwest to southeast. Total stand area for each species was obtained from the GIS software. Most conifers grow elsewhere in California and western North America (Critchfield and Little 1966; Griffin and Critchfield 1976; Hickman 1993) and extend into northern Baja California (Minnich 1987a; Minnich and Franco-Vizcaíno 1998). Statements on substrate are based on the Southern California Areal Mapping Project (SCAMP 2000). Place names are given in Table 1.

Closed-cone conifer forest. Closed-cone conifer forest includes three taxonomic groups: serotinous pines in *Pinus* subsect. *oocarpae* (*Pinus attenuata* Lemmon, *P. muricata* D. Don; taxonomy and variation reviewed in Millar 1986), the partially serotinous *Pinus* sect. *sabinianae* (big-cone pines, *P. coulteri* D. Don and *P. torreyana* Carrière), and two cypresses, *Cupressus arizonica* E. Greene ssp. *arizonica* of the *C. arizonica* complex and *C. forbesii* Jepson (Rehfeldt 1997). *Pinus coulteri* and *P. torreyana* are treated here due their similar fire ecology to species in *Pinus* subsect. *oocarpae* (Haller 1986) and cypresses (Vogl et al. 1988). However, the big-cone pine *P. sabiniana* Douglas is treated as a member of foothill woodland. Closed-cone conifer forests grow in chaparral with stand-replacement fires resulting in spatially synchronized even-aged, short-lived stands. Distributions in southern California are fragmented, with stand boundaries frequently unrelated to local environmental gradients due apparently to stochastic recruitment failures after fire (Vogl et al. 1988). Nearly all closed-cone conifers are found in monospecific stands.

Pinus muricata D. Don (937 ha, Fig. 3).—Small, compact stands of bishop pine are found within 20
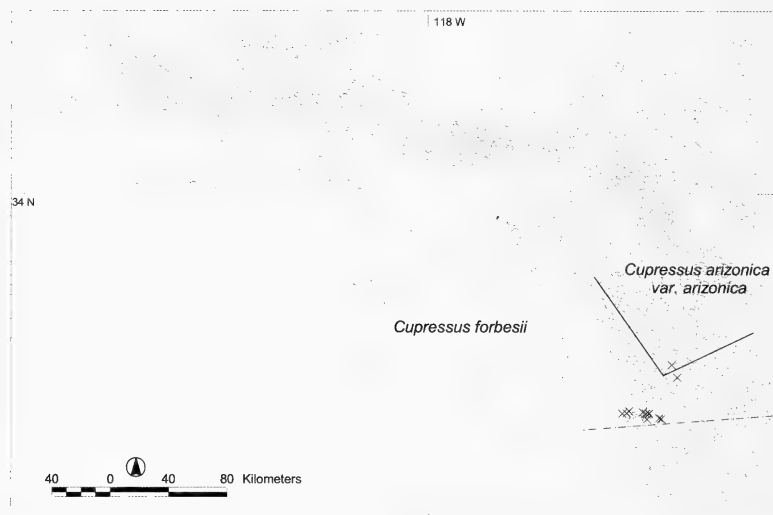
Fig. 4. The distribution of *Cupressus arizonica* var. *arizonica* and *C. forbseii*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

km of the Pacific Coast in the Purisima Hills and the west end of Santa Ynez Mountains. Offshore stands include two colonies on Santa Rosa Island and larger stands on Santa Cruz Island. Mainland stands grow on diatomaceous shales or Careaga sandstones, which produce shallow, highly acid soils with high water-holding capacity (Schoenherr 1992). Island stands grow on a variety of substrates (Vogl et al. 1988). While the AAP ranges from 35–55 cm, fog drip is important to the seasonal distribution of soil moisture (Vogl et al. 1988). Bishop pine grows between 200 and 400 m within the range of coastal low clouds in summer (DeMarrais et al. 1965). The concentration of stands on exposed ridgetops and western exposures optimize foliar fog condensation in strong northwesterly winds of the marine layer. Low temperatures reduce summer transpiration. Bishop pine has recently sustained heavy mortality from needle blight caused by *Dothistroma septospora* (Ades et al. 1992). Most stands on Santa Cruz Island have been degraded or extirpated by grazing and rooting of feral sheep and pigs since 1855 (Brumbaugh 1980; Minnich 1980). The designation of *P. remorata* Mason for trees on Santa Cruz Island has been merged with *P. muricata* (Millar 1986).

Pinus attenuata Lemmon (721 ha, Fig. 3).— Scattered even-aged stands occur in the San Bernardino Mountains from City Creek to Government Peak between 1000 and 1400 m. A VTM error showing a large stand on Keller Peak was a confusion for juvenile *P. coulteri* stands regenerating from fire about 1905 as seen in 1938 aerial photographs. Knobcone pine grows on concave summits and ridges of granitic substrate with thin chaparral dominated by *Adenostoma fasciculatum* Hook. & Arn., *Quercus wislizeni* A.DC., and *Arctostaphylos glandulosa* Eastw. (Minnich 1999). While almost

all stands were burned in 1938, 1956, and 1970, there was abundant post-fire regeneration in the same areas. Two colonies grow in the Santa Ana Mountains at 1000 m: one on the west slope near Pleasants Peak (Vogl 1973), and the other 2 km NE in Hagador Canyon. Both grow on fine-grained, acidic soils associated with hydrothermally altered volcanics (Vogl et al. 1988). The AAP ranges from 50 to 80 cm. Supplemental soil moisture from fog drip is seasonally phased with wet soils from winter storms and may not reduce drought stress in summer. Coastal stratus at the elevations of *P. attenuata* is most frequent in late spring when fog drip totals reach 10 cm per month (Vogl 1973). The climate is warm and dry in summer because stands lie above the marine layer (normally <600 m, DeMarrais et al. 1965).

Cupressus forbesii Jepson (268 ha, Fig. 4).— This Baja California species grows on north-facing slopes between 200 and 1200 m at four localities: an isolated stand in Gypsum Canyon in the northern Santa Ana Mountains, and at Guatay, Tecate Peak, and Otay Mountain in San Diego Co. (AAP, 40–70 cm). Tecate cypress was reported from Hot Springs Mountain in 1880 (Griffin and Critchfield 1976). The Tecate Peak and Otay Mountain stands grow on alkaline clay soils derived from gabbro basalts rich in iron and magnesium (Zedler 1981; Schoenherr 1992). The stand at Guatay grows on granite. The Gypsum Canyon stand grows on Paleocene sandstone, where trees over 200 years old were recorded on canyon floors (Schoenherr 1992). It was not shown in Griffin and Critchfield (1976), although the stand was recorded on VTM quadrangle maps. Gene frequency data shows that genetic distance was not significantly associated with geographic distance between populations (Truesdale and McClenaghan 1998). Variable fire intervals
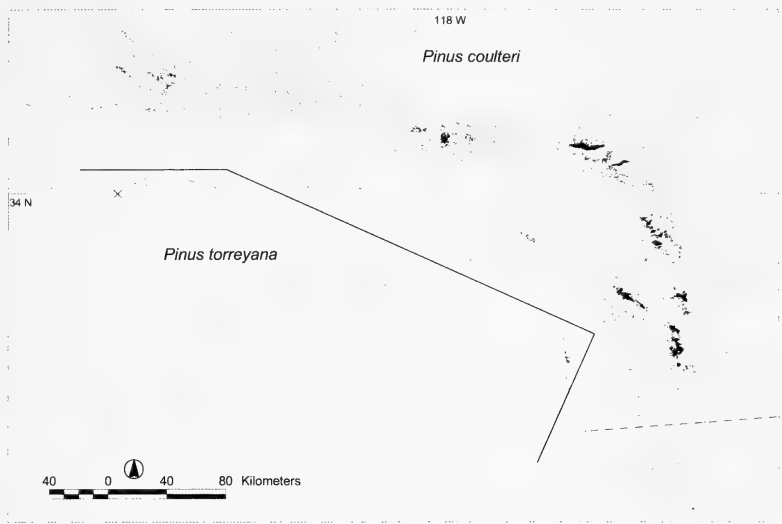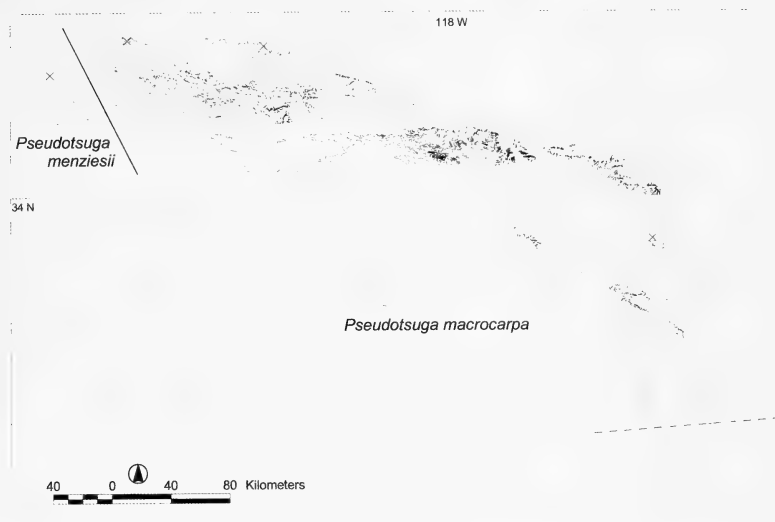
FIG. 5. The distribution of *Pinus coulteri* and *P. torreyana*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

over long-time scales encourage small-scale extinctions and reinvasions (Zedler 1981). Stand degradation may be rare because only 6.0% of the chaparral sustained fire intervals shorter than 20 years during 1920–1972 (Minnich and Chou 1997). The Gypsum Canyon stand regenerated well after a stand-replacement fire in 1948 (Griffin and Critchfield 1976). In northern Baja California, hundreds of even-aged groves grow in a fine-grained chaparral patch mosaic of numerous small burns (Minnich and Chou 1997).

Cupressus arizonica E. Greene *ssp. arizonica* Reyfeldt (5.3 ha, Fig. 4).—A single stand grows on a chaparral-covered west-facing slope of Mt. Cuyumaca near Japacha Peak at an altitude of 1400 m (AAP, 75 cm). Discriminant analysis of 15 genetic traits align the Cuyumaca cypress population in the *C. arizonica* spp. *arizonica* complex which occurs in Arizona and northwestern Mexico; the Cuyamaca population may also occur among inbred lines (Rehfeldt 1997). The nearest stand occurs in the southern Sierra Juárez of northern Baja California (Broder 1963). This tree was formerly classified as *C. stephensonii* C.B. Wolf and *C. arizonica* var. *stephensonii* (C. B. Wolf) Little.

Pinus coulteri D. Don (33,587 ha, Fig. 5).—A near endemic to California, Coulter pine is most widespread in the southern part of the state. It grows between 1000 and 2300 m on steep, concave slopes in association with dense chaparral and scrubby thickets of *Quercus chrysolepis* Liebm., mostly on windward escarpments (AAP, 40–100 cm). Coulter pine responds to stand-replacement burns with high colonizing ability and reproductive effort, with mass post-fire recruitment from seed release from partially serotinous cones, leading to even-aged stands (Borchert 1985; Vogl et al. 1988; Minnich 1999). Mixed-aged stands with arboreal

subcanopy of *Q. chrysolepis* or *Q. kelloggii* Newb. occur on gentle slopes >1300 m (cf. Sawyer et al. 1988). Trees exhibit parallel decreasing cone serotiny with increasing elevation as stands shift from chaparral to oak woodlands (Borchert 1985). It is common in the northern Sierra Madre and San Rafael Mountains, and locally in the Santa Ynez Mountains. After a gap of 150 km, it recurs at Big Tujunga Canyon in the western San Gabriel Mountains and extends eastward into desert slopes at Rock Creek and coastal slopes to Crystal Lake. In the San Bernardino Mountains, Coulter pine is scattered across the southern escarpment east of Waterman Canyon. A continuous belt covers desert drainages from Lake Arrowhead to Holcomb Creek. It is extensive in the San Jacinto, Santa Ana, Hot Springs, Volcan, Palomar, and Cuyamaca Mountains but is not known from the Santa Rosa Mountains. The southernmost populations grow on Los Pinos Mountain. Stands tend to occur on granitic and sandstone substrates that weather into deep soils having secure moisture retention for post-fire recruitment. In drier ranges, where there is greater chance of reproductive failure from drought, Coulter pine frequently survives fire on bedrock slopes, similar to stands in Baja California (Minnich 1987). In spite of comparable climate and topography, Coulter pine does not occur in permeable Precambrian metamorphic gneisses and schists, including the Pelona Schist, that are extensively exposed in the Liebre, Frazier, and Alamo Mountains, as well as the eastern San Gabriel and western San Bernardino Mountains. It is also absent from extensive Eocene marine shales in Ventura County. Coulter pine sustained heavy mortality from insect predations during drought in 1989–1991. Mortality rates as high as 50 ha^{-1} were recorded in the San Jacinto Mountains (Savage
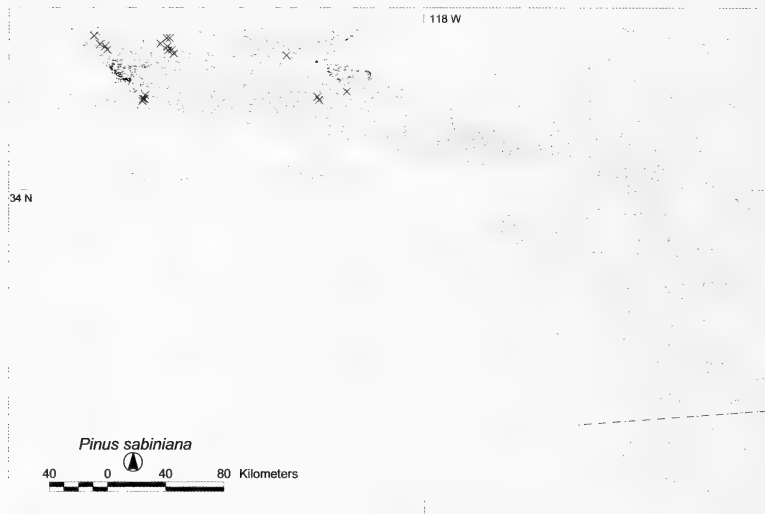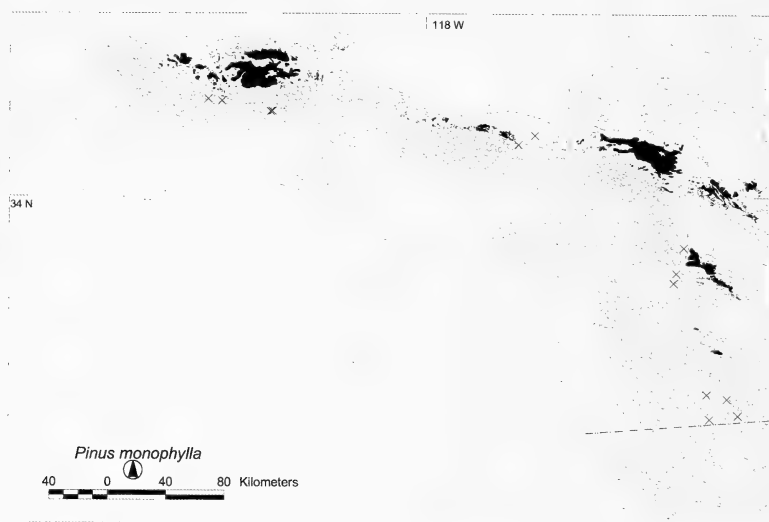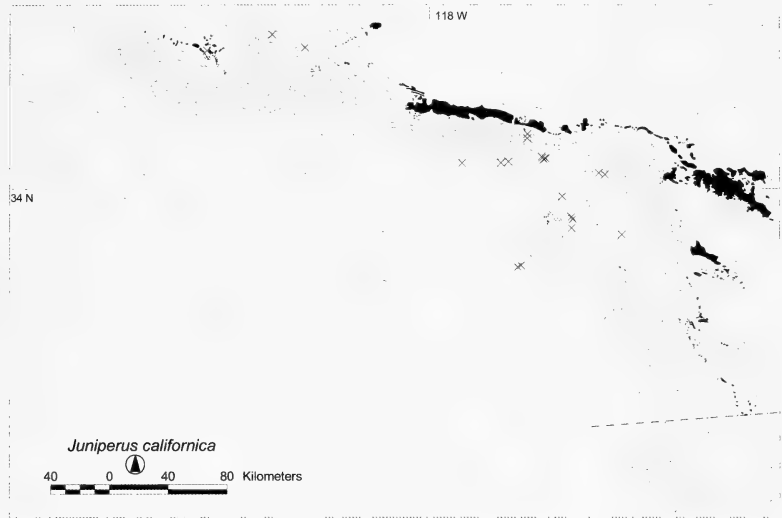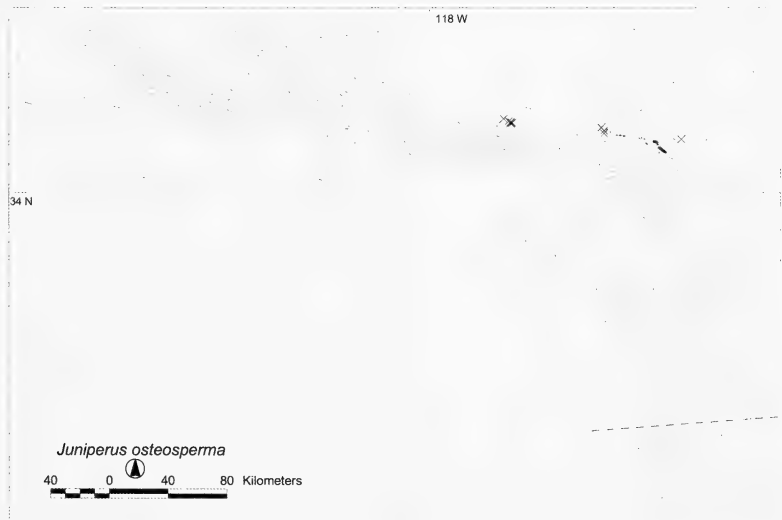
FIG. 6. The distribution of *Pinus sabiniana*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

1994). There were few changes in its range since the VTM survey.

Pinus torreyana Carrière (391 ha, Fig. 5).—The rarest pine in the world (Griffin and Critchfield 1976), Torrey pine occurs at only two localities near the ocean. One includes two stands spanning 6.0 km on rapidly eroding coastal bluffs incised into Eocene sandstone in San Diego Co.: a compact forest at Torrey Pines State Reserve and a fragmented population near Torrey Pines State Beach. The other locality is a 1.0 km forest growing in several ravines cut into upper Miocene sandstone above Beechers Bay on Santa Rosa Island, 270 km to the NW. Prescribed burn experiments shows that severe or fatal fire damage is followed by mass recruitment associated with seed dispersed from serotinous cones, similar to *P. coulteri* (Wells and Getis 1999). The low AAP of 25–35 cm at both localities is supplemented by fog drip (Schoenherr 1992) and is offset by low summer transpiration rates. Haller (1986) proposes that the island population be named *P. torreyana* ssp. *insularis* on the basis of gross morphology and garden plantings. Pollen grains in a sediment core taken from an estuary on Santa Rosa Island indicate that *P. torreyana* has been continuously present there since the middle Holocene (Cole and Liu 1994).

Foothill woodland. Foothill woodland consists of open parks of deciduous and evergreen oaks (*Quercus lobata* Nee, *Q. douglasii* Hook & Arn., *Q. agrifolia* Nee, *Q. wislizeni* A. DC.), scattered shrub cover, and exotic annual grassland (Griffin 1988). The California endemic *Pinus sabiniana* has an extensive range on foothill slopes encircling the Central Valley that are characterized by hot summers and an AAP of 30–60 cm.

Pinus sabiniana Douglas (3,931 ha, Fig. 6).—

Gray pine grows in the San Rafael Mountains from Lazaro Canyon to Zaca Ridge. Colonies extend inland along Manzanita Creek and Sulphur Spring Canyon to Hurricane Deck where it grows on upper Cretaceous bedrock exposures. It is common in the Liebre Mountains. Botanical collections near Lake Piru mark the southern limit of the species. In the San Rafael Mountains, gray pine is found in mixed-aged stands, the trees apparently surviving understory fires. In the Liebre Mountains, many stands are even-aged due to stand-replacing chaparral burns, the recruitment establishing from seed released by serotinous cones. The distribution of gray pine is similar to that on VTM quadrangle maps.

Mixed evergreen forest. Mixed evergreen forest, which comprises long-lived evergreen coniferous and hardwood trees, is extensive in the coastal ranges of northern and central California (Sawyer et al. 1988). In southern California, this type consists of the *Pseudotsuga macrocarpa–Quercus chrysolepis* phase. One outpost of *P. menziesii* grows near Lompoc.

Pseudotsuga menziesii (Mirbel) Franco var. *menziesii* (4.2 ha, Fig. 7).—A single colony occurs in a moist canyon in the Purisima hills (Griffin 1964). It is surrounded by chaparral and *Pinus muricata* D. Don stands. This population receives abnormally low precipitation for the species (AAP, 40 cm), and apparently survives on cool summers and the high water table of the watercourse. The nearest stand lies 150 km NW in the Santa Lucia Mountains.

Pseudotsuga macrocarpa (Vasey) Mayr (22,232 ha, Fig. 7).—A southern California endemic, this long-lived tree (Bolton and Vogl 1969; McDonald and Littrell 1976; Haston and Michaelson 1994) has a fragmented distribution of compact groves in steep canyons, north-facing slopes, and cliff faces

Fɪɢ. 7.   The distribution of *Pseudotsuga macrocarpa* and *P. menziesii*. Shaded areas mapped from aerial photographs.
x = botanical collections or field vouchers.

between 1000 and 2200 m. Big-cone Douglas fir grows largely on windward escarpments, especially on slopes with high rates of erosion associated with fault-shattered substrate (AAP, 50–110 cm). The small-scale map in Griffin and Critchfield (1976) portrays a more continuous distribution than depicted on VTM quadrangle maps and Figure 7.

Rare colonies in La Brea Creek in the northern Sierra Madre Mountains are 20 km disjunct from abundant stands on Figueroa and Big Pine Mountains of the San Rafael Mountains. Numerous groves occur over an extensive area between the San Rafael Mountains and Lake Piru. Between Pine Mountain Ridge and Mount Pinos, big-cone Douglas fir is surprisingly abundant in semiarid badlands eroding into Quaternary alluvial terrace deposits and Pliocene sedimentary rocks, where it is associated with *Pinus monophylla* Torrey & Frémont. It is scarce on the undissected slopes of Mt. Pinos, Frazier Mountain, and Alamo Mountain, but common in canyons along the San Andreas fault in the San Emigdio and Liebre Mountains. Extraordinary stands grow at 600 m in the eastern Santa Susana Mountain badlands on Pliocene and upper Miocene marine sandstones and shales. Big-cone Douglas fir is extensively distributed in deeply incised canyons cutting into fault-shattered substrate of the San Gabriel Mountains. Continuous forests (stands >500 ha) are found near Mt. Wilson and Mt. San Antonio. In the San Bernardino Mountains, colonies span the southern escarpment and desert drainages west of Lake Arrowhead. In the Peninsular Ranges, big-cone Douglas fir is mostly restricted to escarpments of active faults. Along the Elsinore fault, it is common in the Santa Ana, Palomar, and Volcan Mountains. It is uncommon along the San Jacinto fault from Bautista Mountain to Thomas Mountain. *Pseudotsuga macrocarpa* is not known from the

Santa Rosa, Hot Springs, Cuyamaca, and Laguna Mountains.

Although big-cone Douglas fir survives recurrent fire in association with arboreal *Quercus chrysolepis* in convex canyons, it has recently sustained widespread extirpations from wind-driven chaparral fires. In the eastern San Gabriel and San Bernardino Mountains, stand-replacement burns have exceeded recolonization rates, resulting in a net extirpation of 18% of forests since the 1938 aerial photographs (Minnich 1999). Current losses may be a natural perturbation due to variability in the fire process. However, fires should not act to synchronize stand age structure, nor produce extensive changes in the spatial extent of stands over short time scales because subcanopy burns result in continuous recruitment and high tree survivorship over multiple fire cycles. The extirpation of *P. macrocarpa* is not due to excess fuel build-up because regional fire intervals have changed little under fire suppression (Minnich and Chou 1997; Minnich 1999). Alternatively, the elimination of stands may be related to the nonrandomization of large fire occurrences to the severest weather conditions by suppression, notably Santa Ana winds (Minnich and Chou 1997). In the 19th century, forests were burned by low intensity fires persisting for months (Minnich 1987b). VTM stands have been reduced or extirpated in many areas of the Cobblestone and Topatopa Mountains, the eastern Transverse Ranges, Lake Hemet, Mt. Palomar, and Volcan Mountain.

Pinyon-juniper woodland. Pinyon-juniper woodland, which comprises *P. monophylla, Juniperus osteosperma* (Torrey) Little and *J. californica* Carrière, is widespread on leeward mountain slopes and along the margin of the Mojave and Sonoran Deserts. Trees grow with open shrub cover of Great
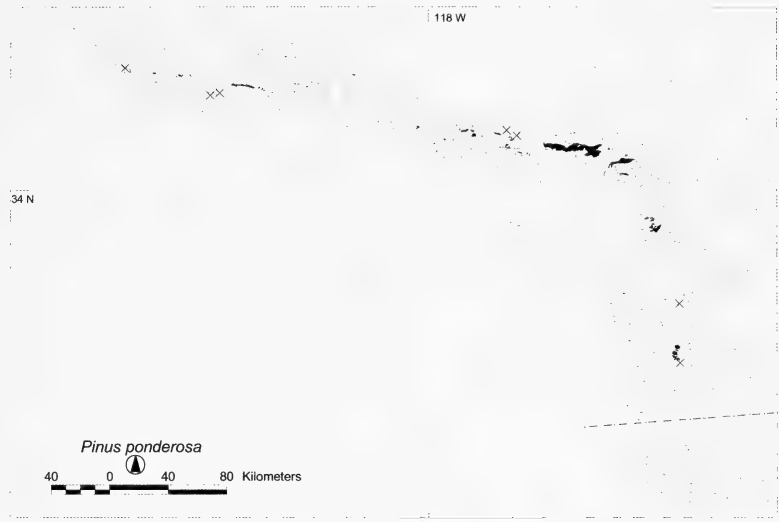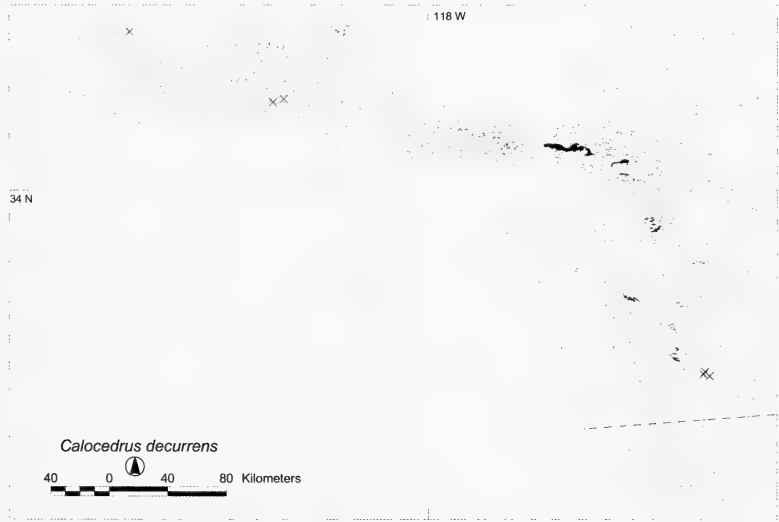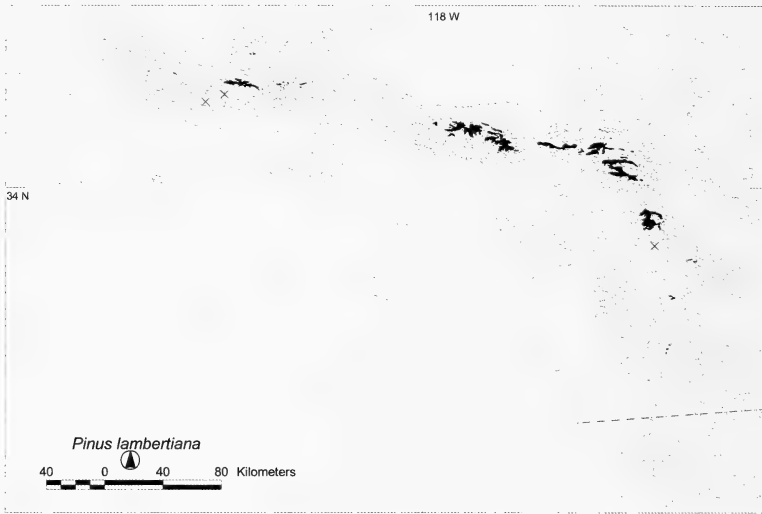
Fig. 8. The distribution of *Pinus monophylla*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

Basin sage scrub, desert chaparral, and Mojave Desert scrub. *Pinus quadrifolia* occurs in chaparral in inland coastal slopes.

Pinus monophylla Torrey & Frémont (156,815 ha, Fig. 8).—Single-leaf pinyon is found on leeward escarpments from 1300–2700 m (AAP, 20–50 cm). Extensive stands occur in the plateaus of the upper Cuyama River, Lockwood Valley, Sisquoc River, and Sespe Creek, including a few sandstone outcrops in the Topatopa Mountains. It is widespread on the northern escarpments of the San Gabriel and San Bernardino Mountains. A small population grows on fire-resistant cliffs in Cattle Canyon on the coastal slope of Mt. San Antonio (Thorne 1988). It is common in Joshua Tree National Park, especially on granites. In the Peninsular Ranges, *P. monophylla* is widespread only in the Santa Rosa Mountains from Pinyon Flat to Rabbit Peak. Small stands occur in the northeastern San Jacinto Mountains and the summits of Pinyon Ridge and Whale Peak. Outliers grow on Mt. Laguna and east of McCain Valley. Single-leaf pinyon is extensive above 1300 m in the northeast Mojave Desert. In the Colorado Desert, small stands cover two summits of the Eagle Mountains and another grows on the summit of the Coxcomb Mountains.

Based on needle resin duct morphology, it had been proposed that *P. monophylla* be divided into two varieties, *P. monophylla* var. *monophylla* in the northern Mojave Desert and *P. monophylla* var. *californiarum* in the Sierra Nevada and southern California, but *The Jepson Manual* does not recognize varieties of single-leaf pinyon (Lanner 1999).

Since the VTM survey, stand-replacement burns have removed single-leaf pinyon stands at Rock Creek and near Wrightwood in the San Gabriel Mountains, in the northern San Bernardino Mountains, Pinyon Flat in the Santa Rosa Mountains, and

northwestern Joshua Tree National Park. However, the distribution of single-leaf pinyon appears to be stable because low primary productivity rates associated with low AAP limit fire intervals in the order of centuries, and gradual recolonization is seen in burns dating to the early 19th century (Wangler and Minnich 1996). Establishment does not appear to be limited by fire size due to efficient seed dispersal and caching by birds and rodents (VanderWall 1997).

Juniperus californica Carriére (149,464 ha, Fig. 9).—California juniper is common between 800 and 1700 m on alluvial bajadas extending onto the Mojave Desert from the Sierra Nevada and the north slope of Transverse Ranges to Joshua Tree National Park. It is locally abundant on the leeward flank of the Peninsular Ranges, with extensive stands in the Santa Rosa Mountains. Outposts occur in semiarid coastal drainages, including the Cuyama River, upper Soledad Canyon, alluvial fans of the Transverse Range (Azusa, Lytle Creek, Redlands), and in the Riverside-Perris Plain (Temescal Canyon, Lake Mathews, Gavilon Hills, Perris, Lakeview Mountains, Aguanga). A few trees occur near the coast in the Santa Monica Mountains (Raven and Thompson 1966) and in the Santa Ana Mountains. The AAP ranges from 20–40 cm.

Extensive stands mapped by VTM workers in the Mojave Desert have been denuded by fires carried by exotic grassland dominated by *Bromus madritensis* L. and *Schismus barbatis* L. (Lovich and Bainbridge 1999). Stands have also been cleared for development.

Juniperus osteosperma (Torrey) Little (1,619 ha, Fig. 10).—Utah juniper occurs in the eastern Transverse Ranges between 1500 and 2200 m (AAP, 20–35 cm). In the San Gabriel Mountains, a few stands grow near Phelan. It is common on the northern
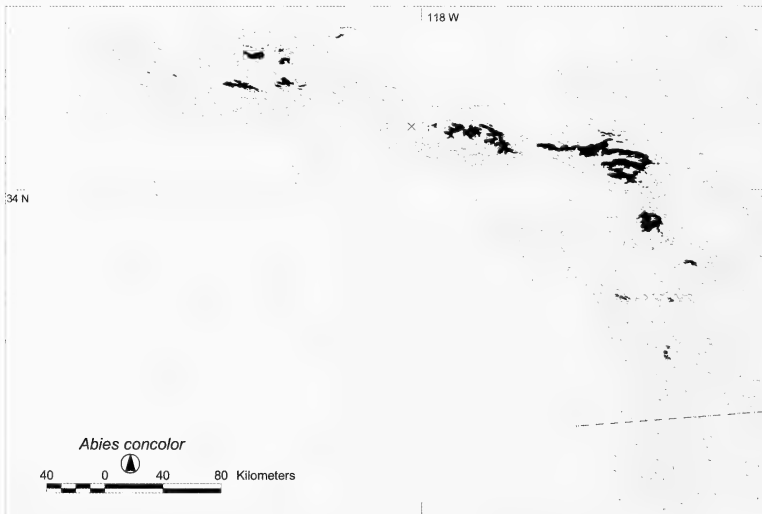
FIG. 9. The distribution of *Juniperus californica*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

escarpment of the San Bernardino Mountains from Grapevine canyon to Tip Top Mountain, with stands concentrating on carboniferous calcite and dolomite marbles. Large stands have been extirpated by the development of limestone quarries. Botanical collections of F. C. Vasek (UCR) indicate that most specimens are intergrades with *J. occidentalis* Hook. var. *australis* and *J. californica* Carrière. Utah juniper is common in the higher ranges of the northeast Mojave Desert.

Pinus quadrifolia Parl. (668 ha, Fig. 11).—An endemic to the Peninsular Ranges of southern California and northern Baja California, four-needle pinyon grows in chaparral from 1300–1800 m (AAP, 35–55 cm). The largest stands occur at Tho-

mas Mountain, southern Garner Valley, and Vandeventer Flat in the southern San Jacinto Mountains. Small stands occur 55 km south on Mt. Laguna and in McCain Valley. Time-series aerial photographs in the Sierra San Pedro Mártir show that stand-replacement burns are followed by rapid recolonization in mature chaparral. Since the VTM survey, large populations have established in 80-yr old chaparral at the south end of Thomas Mountain. Pinyon pines are not known for cone serotiny, and recruitment appears to be dependent on seed cached by birds and mammals.

Lanner (1999) proposes that *P. quadrifolia* is a hybrid between *P. monophylla* and *P. juarezensis* (a five-needle pinyon). The designation is based on

FIG. 10. The distribution of *Juniperus osteosperma*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

FIG. 11. The distribution of *Pinus quadrifolia*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

large variation in needle number, leaf resin canal number, twig hairiness and stomate position in populations of the La Rumerosa Plain near the Mexican border. However, *P. monophylla* and *P. quadrifolia* have strong ecologic and geographic segregation, with *P. monophylla* forming open stands on the desert-facing slopes and *P. quadrifolia* occurring in chaparral on coastal escarpments, their ranges broadly overlapping only on the La Rumerosa plain (Minnich 1987a). Monospecific *P. quadrifolia* woodlands, such as those on coastal slopes of the Sierra San Pedro Mártir or on Thomas Mountain, should be investigated for their morphological and genetic properties. *Pinus juarezensis* is not recognized in *The Jepson Manual* (Hickman 1993).

Mixed-conifer forest. While the modest elevations of the southern California mountains limit the spatial extent of mixed-conifer forest, the broad distribution of dominant tree species resembles those in the Sierra Nevada (Barbour and Minnich 2000). Mesic "westside" forests of *P. ponderosa, P. lambertiana, Calocedrus decurrens* and *Abies concolor* grow on windward slopes (AAP, 75–115 cm). Drier "eastside" forests of *P. jeffreyi, A. concolor* and *J. occidentalis* grow on leeward slopes (AAP, 30–75 cm). "Eastside" forests also cover thin soils on windward flanks of dissected ranges. Mixed-conifer forest grows in areas with low combustible shrub biomass, mostly at higher altitudes above the chaparral belt (>1500–2200 m) or in shrub-free basins within the chaparral belt (Minnich 2001). Subcanopy consists of open cover of montane chaparral dominated by *Arctostaphylos pringlei* C. Parry, *A. patula* E. Greene, *C. cordulatus* Kell., *Ceanothus integerrimus* Hook. & Arn., *Cercocarpus ledifolius* Nutt., *Chrysolepis sempervirens* (Kell.) Hjelmq., and *Rhamnus californica* Eschsch. Important hard-

wood associates are *Q. chrysolepis* and *Q. kellog-gii*. Mixed-conifer forest is not found in the Santa Ana Mountains despite summit altitudes of 1700 m.

Pinus ponderosa Laws (22,841 ha, Fig. 12).—In southern California, VTM workers identified Jeffrey pine as *P. ponderosa* var. *jeffreyi,* resulting in ambiguous differentiation between *P. ponderosa* and *P. jeffreyi* (Griffin and Critchfield 1976). VTM maps show confusion in the Transverse Ranges where *P. ponderosa* was erroneously shown to be extensive. In our survey, ponderosa pine was distinguished from Jeffrey pine on aerial photographs based on deeper yellow-green (blue-green) foliage and more cylindrical (conical) shape of canopies of ponderosa (Jeffrey) pine. In the field we noted for foliage color and yellow (brown) immature cones of ponderosa (Jeffrey) pine. The reduction in the spatial extent of ponderosa pine in Fig. 12 compared to VTM maps is consistent with its decreasing importance southward in California.

Ponderosa pine is most abundant in areas with high AAP and deep soils between 1400 and 2100 m. Small colonies cover the San Rafael Mountains, and it is common along Pine Mountain Ridge. Ponderosa pine appears to be absent from Mt. Pinos, Frazier Mountain, and Alamo Mountain (Vogl and Miller 1968). We saw a few stems on groundwater seeps along the San Andreas fault in Cuddy Valley and north of Mt. Pinos. A monotypic stand covers Sawmill Mountain in the Liebre Mountains. Ponderosa pine covers small basins or gentle summits in the San Gabriel Mountains. The largest stands grow from Mt. Waterman to Mt. Islip and near Crystal Lake (cf. Thorne 1988). The only extensive stand is a 30-km belt along an old erosion surface of weathered granite in the western San Bernardino Mountains. Trees grow as low as 1100 m, compa-
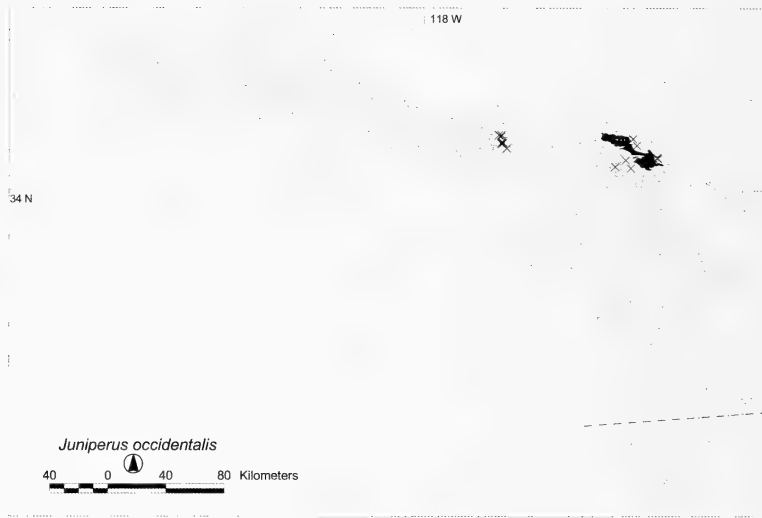
FIG. 12.   The distribution of *Pinus ponderosa.* Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

rable to other "westside" stands in the Sierra Ne-vada. Large stands grow at Barton Flats and Mill Creek. In the Peninsular Ranges, ponderosa pine occurs on the west flank of Mt. San Jacinto. To the south, a small colony grows at Doone Valley on Mt. Palomar, and a single tree 30 m tall straddles an arroyo on Hot Springs Mountain at 1600 m. Stands on Mt. Cuyamaca represent the southern limit of the species along the Pacific Coast.

Calocedrus decurrens (Torrey) Florin (13,952 ha, Fig. 13).—The range of incense cedar is similar to *P. ponderosa,* except that it concentrates on stream courses from 1100 to 2200 m. It occurs lo-cally in the San Rafael Range and in one north-facing canyon of the northern Sierra Madre. Stands

are common from Pine Mountain Ridge to Alamo Mountain, and from the San Emigdio Mountains to the Tehachapi Mountains. It grows in canyons throughout the San Gabriel Mountains. In the San Bernardino Mountains, incense cedar forms wide-spread understory thickets in dense ponderosa pine forest from Crestline to Running Springs, in Barton Flats, and in Mill Creek, with stands concentrating near watercourses in open forests (Minnich et al. 1995). Subcanopy thickets are also widespread in the northern San Jacinto, Palomar, and Cuyamaca Mountains. Local mature stands grow in the drier Santa Rosa, Hot Springs, Volcan, and Laguna Mountains.

Pinus lambertiana Douglas (53,477 ha, Fig.

FIG. 13.   The distribution of *Calocedrus decurrens.* Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

Fig. 14. The distribution of *Pinus lambertiana*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

14).—Sugar pine is common on steep, mostly north-facing slopes between 1700 and 2700 m. Isolated colonies grow in the San Rafael Mountains, but it is extensive on Pine Mountain Ridge, Cobblestone Mountain, and north-facing cliffs of the Topatopa Mountains. It is rare in the semiarid ranges to the north, except locally on Mt. Pinos. Sugar pine is common across the San Gabriel and San Bernardino Mountains, but is absent on leeward slopes near Wrightwood and Big Bear. In the Peninsular Ranges, it is widespread only on Mt. San Jacinto. Local stands grow on the Santa Rosa, Hot Springs, and Cuyamaca Mountains. It is not known from the Palomar, Volcan, and Laguna Mountains.

Abies concolor (Gordon & Glend.) Lindley

(107,415 ha, Fig. 15).—Vasek (1985) provides evidence that southern California white fir is the Rocky Mountain variety *A. concolor* var. *concolor,* whereas the Pacific coast variety *A. concolor* var. *lowenia* grows in the Sierra Nevada southward to the Tehachapi Mountains. White fir is often dominant on north-facing slopes from 1500 to 2800 m. It grows in the San Rafael Mountains, along Pine Mountain Ridge, and in "eastside" forests covering the Mt. Pinos, San Emigdio, Alamo, Frazier, and Tehachapi Mountains. White fir is found throughout the San Gabriel and San Bernardino Mountains with extensive subcanopy thickets growing in the dense mixed-conifer forests at Lake Arrowhead and Barton Flats (Minnich et al. 1995). The tree is
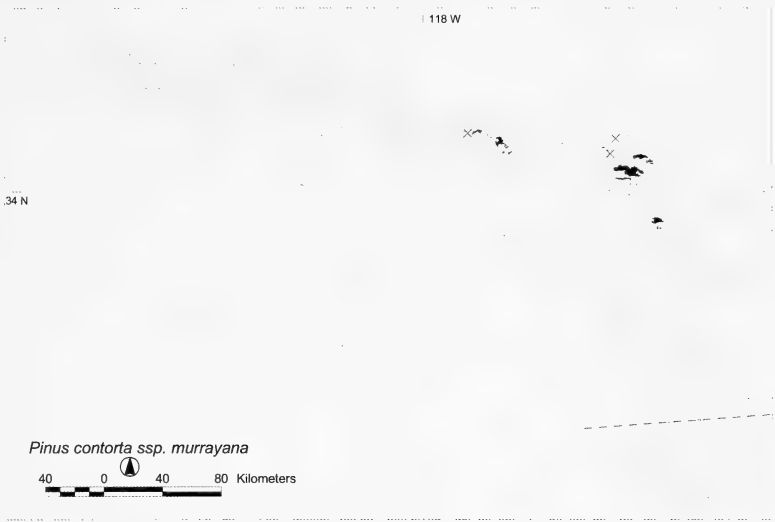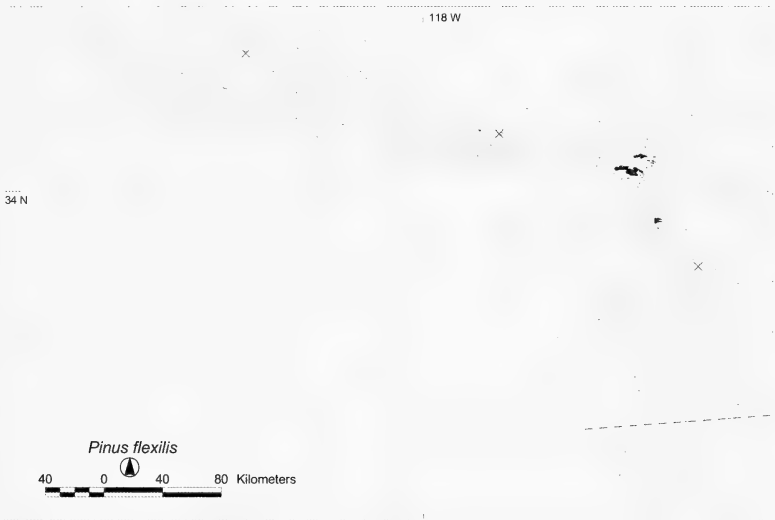

Fig. 15. The distribution of *Abies concolor*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.
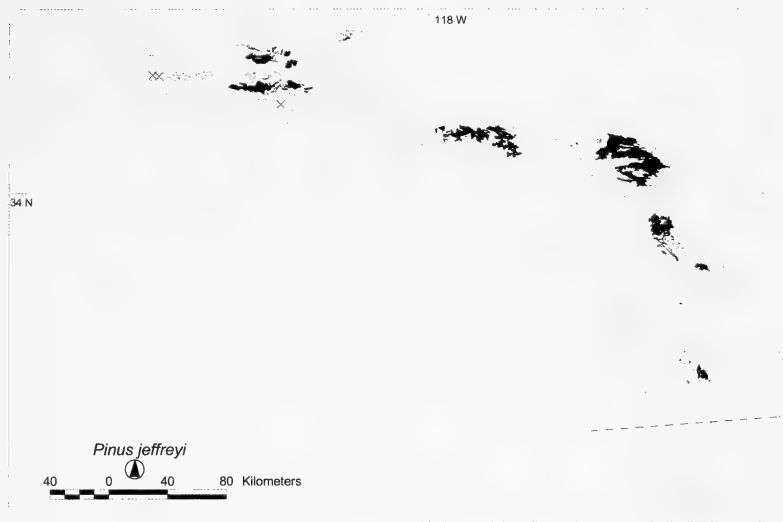
FIG. 16.   The distribution of *Pinus jeffreyi*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

widespread on Mt. San Jacinto, and an invasive subcanopy tree near Idyllwild. Small populations occur on Palm Divide, Santa Rosa Mountain, Thomas Mountain, and Hot Springs Mountain. White fir is invasive in the Palomar and Cuyamaca Mountains. A VTM record of white fir in the Volcan Mountains cannot be confirmed, and it is not known from the Laguna Mountains. The Rocky Mountain variety grows in the Kingston and Clark Mountains of the northeast Mojave Desert.

Pinus jeffreyi Grev. & Balf. (124,551 ha, Fig. 16).—Jeffrey pine is the forest dominant >2000 m in southern California. It also covers local shrub-free basins in the chaparral belt to as low as 1100 m in monospecific stands. Jeffrey pine typically replaces *P. ponderosa* along decreasing precipitation gradients. The confusion of *P. jeffreyi* and *P. ponderosa* by VTM workers resulted in maps erroneously showing *P. jeffreyi* in areas where only *P. ponderosa* occurs.

Jeffrey pine is extensive on Pine Mountain Ridge, Mt. Pinos, Frazier Mountain, Alamo Mountain, and the San Emigdio Mountains. Monotypic stands extend downslope into Lockwood Valley and along the Cuyama River plain to 1300 m. A few trees grow in the San Rafael Mountains. It spans the San Gabriel Mountains and the San Bernardino Mountains east of Lake Arrowhead. Jeffrey pine is common on Mt. San Jacinto, Santa Rosa Mountain, and the summit of Thomas Mountain. It is extensive in nearby Garner Valley at 1400 m, and a large VTM stand to the east was mistaken for *P. coulteri*. A single stand grows on Hot Springs Mountain (it was shown as *P. ponderosa* on VTM maps), but a few trees near Palomar Mountain Observatory appear to be planted. Jeffrey pine is common in the Cuyamaca Mountains and forms monotypic stands on the Laguna Mountain plateau and

adjoining basins. The southernmost population is at Pine Valley at an altitude of 1100 m.

Juniperus occidentalis Hook. var. australis (Vasek) A. Holmgren & N. Holmgren (23,011 ha, Fig. 17).—Sierra Nevada western juniper is found locally on Wright Mountain, Mt. San Antonio, and in Icehouse Canyon in the eastern San Gabriel Mountains. In the San Bernardino Mountains, it is widespread with Jeffrey pine >2100 m on the semiarid plateaus near Big Bear, with stands frequently extending into pinyon-juniper woodland. Ancient trees with dbh >2–3 m are seen from Sugarloaf Mountain to Onyx Summit. Isolated trees occur on San Gorgonio Mountain, the southern limit of the species.

While members of mixed conifer forest exhibit extensive range overlap, species boundaries are invariably congruent at the edge of recent stand-replacement burns. Congruent boundaries also occur at the chaparral ecotone. These trends reflect the similar adaptations of these conifers (tall stature, thick bark) to survive subcanopy burns recurring 2–3 times per century (Minnich et al. 2000). All mixed-conifers are selectively eliminated by stand-replacement fires in chaparral. Since the VTM survey, fire suppression has led increasing fire intervals and stand-densification, with an age-specific trend away from dominance by *P. ponderosa* or *P. jeffreyi*, and toward dominance by juvenile, pole-size classes of *A. concolor* and *C. decurrens* (Ansley and Battles 1998; Minnich 1988; Minnich et al. 1995; Roy and Vankat 1999; Minnich et al. 2000). Increasing fuel loads and stand-densification have led to widespread stand-replacement burns (Minnich 1999; Barbour and Minnich 2000; Minnich et al. 2000), similar to that in the Sierra Nevada (Weatherspoon et al. 1992; McKelvey and Johnston 1992; SNEP 1996). Stands that were

Fig. 17. The distribution of *Juniperus occidentalis*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

logged during the late 19th century, mostly at Lake Arrowhead, Idyllwild, Mt. Laguna and Mt. Cuyamaca (Minnich 1988; Pryde 1984) have densities exceeding 300–500 stems ha⁻¹, or are 1.5 to 6 times that recorded in forests sampled by VTM workers in 1929–1934, and in the Sierra San Pedro Mártir, Mexico, where open parklike forests are produced by intense subcanopy burns at intervals of 50 years without fire control (Minnich et al. 1995, 2000). In southern California, open forests persist on drier leeward slopes with low primary productivity (Minnich et al. 1995) or in steep, dissected ranges with thin soils such as the San Gabriel Mountains. Crown fires have denuded extensive stands (>500 ha units) mapped by VTM workers, with stands being replaced by successional montane shrublands, *Q. chrysolepis* and *Q. kelloggii* (cf. Kauffman and Martin 1990, 1991). Portions of VTM forests were extirpated at Pine Mountain Ridge, Alamo Mountain, Frazier Mountain, as well as Pleasant View Ridge, Prairie Fork, Ontario Peak, and Cucamonga Peak in the San Gabriel Mountains. Extirpations also occurred near Big Bear Lake and Raywood Flat in the San Bernardino Mountains, Mount San Jacinto, Mount Cuyamaca, and the south edge of the Laguna Mountain plateau.

Subalpine forest. Subalpine forest grows on isolated summits >2500 m (AAP, 40–100 cm). Compared to the Sierra Nevada, southern California subalpine forests are floristically depauperate, with only two pine species occurring in the region.

Pinus contorta Loudon ssp. *murrayana* (Grev. & Balf.) Critchf. (11,696 ha, Fig. 18).—In the San Gabriel Mountains, lodgepole pine occurs from Throop Peak to Mt. Baden-Powell, and on summits from Mt. San Antonio to Cucamonga Peak. In the San Bernardino Mountains, it grows on slopes and valley floors at Butler Peak, Sugarloaf Mountain, Holcomb Valley, Bluff Lake, Big Bear, and the upper Santa Ana River. It dominates subalpine forests on San Gorgonio Mountain. The southernmost stands occur on Mt. San Jacinto and Tahquitz Peak.

Pinus flexilis James (6,642 ha, Fig. 19).—Small colonies grow on Mt. Pinos and nearby Cerro Nordeste. In the San Gabriel Mountains, the only major population extends from Throop Peak to Mt. Baden-Powell; a few trees occur 10 km E on Wright Mountain. It is strangely absent from lodgepole pine forests near Mt. San Antonio. In the San Bernardino Mountains, limber pine is common on Sugarloaf Mountain, Onyx Summit, and other semiarid peaks in the upper Santa Ana River where it grows with "eastside" stands of *P. jeffreyi, A. concolor,* and *J. occidentalis.* At Onyx Summit (AAP, 35 cm), limber pine forms ecotones with single-leaf pinyon woodlands, similar to forest zonation in the Great Basin. It is common >2,800 m on Mt. San Gorgonio. In the San Jacinto Mountains, stands grow on Mt. San Jacinto and Tahquitz Peak. Maps of Griffin and Critchfield (1976) show them 15 km too far east. A small population on Toro Peak in the Santa Rosa Mountains is the southern limit of the species.

While subalpine forests in southern California experience numerous small burns initiated by lightning, site-specific mean fire intervals are in the order of centuries (Sheppard and Lassoie 1998). Stands show local patchiness from 19th century stand-replacement burns on the San Bernardino Ridge, Mt. Grinnell (Minnich 1988), and the east face of Mt. San Jacinto. Since the VTM survey, stand-replacement burns have occurred in the upper Whitewater River near Mount San Gorgonio, near Butler Peak, and on Ontario Peak. All burns are regenerating well.

FIG. 18.   The distribution of *Pinus contorta*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

FIG. 19.   The distribution of *Pinus flexilis*. Shaded areas mapped from aerial photographs. x = botanical collections or field vouchers.

DISCUSSION

While distributions viewed statically provide insight into ecological relationships, how a species adapts to an environment can also be evaluated from a synoptic time-series frame of reference. In addition, a regional approach permits the examination of the broadscale status of populations as seen in time- and space-averaging of local scale population dynamics. The assessment of stand dynamics is not straightforward with respect to whether species changes reflect normal biomass removal and accumulations from fire and postfire successions, or whether they reflect long-term directional change. This distinction cannot be made here from a time-series comparison of forest maps

only 70 years apart. However, for the purpose of hypothesis testing of population stability, we propose that vegetation baselines in southern California be interpreted using three fire disturbance models which address key processes or patterns that influence stability.

Shifting population model (closed-cone conifer forests, Pinus quadrifolia *woodland).* The large size of chaparral stand-replacement burns (two to three per century) relative to the size of individual conifer populations tends to synchronize stand age distributions across entire stream drainages, resulting in large temporal variation in their spatial extent at local scales. Stands "disappear" in recent burns, but emerge as even-aged stands in older chaparral

patches, "following" old-growth patch mosaics. To evaluate the stability of shifting populations, it may be best to search for postfire recruitment failures (stands which fail to reestablish after burns, e.g., Zedler 1981; Vogl et al. 1988) because individual fires can eliminate both the adult population and the seed bank, resulting in local extinctions. *Pinus quadrifolia* forests have these characteristics, but individual stands are mixed-aged because recruitment is continuous through successions.

Standing population model (mixed-conifer forest, mixed-evergreen big-cone Douglas fir forest, gray pine foothill woodland). The canopy layer persists through recurrent subcanopy fires (two to three per century), resulting in "standing" or fixed distributions with small local fluctuations. Although trees recruit continuously, stands undergo intense selective elimination of sapling and polesize trees from subcanopy fires, with a few mid-size trees incrementally joining the canopy layer between fire sequences, producing mixed-aged overstory. Discrete age mosaics in the canopy layer are rare because stand-replacement burns are rare. Stands occupy sites safe from dense shrub subcanopy that normally produce stand-replacement fires, especially chaparral. Stability can be evaluated from the long-term expansion or contraction of "standing" tree populations over multiple fire cycles. A key factor may be the spatial extent of individual stand-replacement burns, and whether stand attrition is balanced by recolonization. Since the initiation of fire suppression, stand-replacement burns have frequently exceeded 1000 ha, whereas patches created by crown fires rarely exceed 10 ha without fire control in mixed-conifer forests of the Sierra San Pedro Mártir of Baja California (Minnich 1999; Minnich et al. 2000).

Patch mosaic population model (pinyon-juniper woodland, subalpine forest). Low productivity rates and stand structure result in long interval subcanopy to canopy fires (return intervals <1 per century). Stand mortality is high because the flame front both consumes tree canopy, and the thin bark of partially burned conifers results in fatal cambium damage. Stands exhibit discrete inter-stand age structures arrayed in a patch mosaic. Individual stands are mixed-aged due to continuous recruitment, especially in shade-tolerant species such as *P. monophylla* and *P. flexilis*. Trees exhibit little change in broadscale distributions, but patches appear in the form of recent stand-replacement burns. These patches fade after 50–100 years as recruitment gradually establishes closed canopy. Older age class boundaries are subtle because fire return intervals scale at several per millennia. Trees are longer-lived than members of closed-cone conifer forests and stability is harder to establish over time scales of a century. The potential for destabilization of forests may again be reflected in the size of stand-replacement burns.

How can these population models be applied to long-term species changes? While the distribution of conifer forests has been altered by fire over the past century, the stability of these ecosystems cannot be judged alone by the historical severity and spatial extent of fires. Fire regimes in California forests are an outgrowth of cumulative fuel build-up scaling from several decades to centuries, the time lag between fuel accumulation and burning making fire self-limiting, and time-dependent (Minnich and Chou 1997; Minnich et al. 2000). The site-specific properties of fire (intervals, intensities, removal of biomass) vary with climate, primary productivity, and fuel accumulation rates and exert profound selection in tree species distributions depending on their life history traits (Veblen et al. 1991; Christensen 1993; Johnson and Gutsell 1994). Forest ecosystems tend to burn most frequently in areas with highest productivity (cf. Knight 1987; Veblen et al. 1991). In southern California growth rates are proportional to mean annual rainfall, except at highest elevations (>ca. 2300 m) where productivity is limited by short growing seasons. Fire return intervals range from two to three times per century in closed-cone, mixed-evergreen, and mixed-conifer forest on moist coastal windward slopes (Minnich and Chou 1997; Minnich et al. 2000) to <1 per century in pinyon-juniper woodland on semiarid leeward slopes (Wangler and Minnich 1996) and subalpine forests on highest summits. Fire severity and conifer mortality rates also vary because conifer species are associated with divergent subcanopy vegetation and vertical distribution of fuels (Minnich 2001).

The role of climate variability on fire regimes and long-term directional change of forests is a gradual process because fire outcomes are an outgrowth of long-term vegetation successions and fuel build-up. Directional vegetation changes also lag behind climatic perturbations because selection processes that result in changes in recruitment and successions require several generations to translate into mature phases of the vegetation.

Fire suppression, which is unprecedented in ecological history, may produce rapid change, especially where fires have been excluded from forests for extended periods. In addition, the intensity of large fires may have increased because suppression both encourages excessive fuel build-up where fire intervals have lengthened and selectively restricts uncontrolled fires to the severest weather conditions (Minnich and Chou 1997). Forests experiencing shifting or patch mosaic population dynamics normally experience high fire severity and mortality, and how changes in fire intensity with suppression would change the stand-replacing fire regime is unclear. Fire intervals in chaparral and closed-conifer forests have been stable with or without suppression (Minnich and Chou 1997). Unproductive patch mosaic model ecosystems may be

well within presuppression fire-free periods. In spite of local removal of forests by stand-replacement burns, the spatial extent of conifer species having shifting and patch mosaic population dynamics has changed little during the 20th century. The demonstration of long-term change in these ecosystems would require evidence that replacement recruitment rates are dependent on the survivorship of the adult population. Reduced reproductive potential in short interval fire recurrences may be infrequent because the turnover of patch mosaics is dependent on cumulative fuel build-up. Invasive exotic annual grasses that produce abundant cured fuel, including *Bromus madritensis* L., *B. diandrus* Roth, and *Avena barbata* Link, may increase the frequency of short-interval burn sequences and degradation of coastal sage scrub and chaparral (Freudenberger et al. 1987; Minnich and Dezzani 1998). However, invasive species are generally limited to coastal valleys and lower foothills far removed from conifer ecosystems. Directional change in closed-cone conifers may arise from post-fire recruitment failure due to short-term extreme environmental conditions, such as drought, but on the basis of chance extreme conditions seldom coincide with fire cycles over long time scales.

Recent fire history suggests that the greatest potential for directional vegetation change may occur in ecosystems having "standing" population dynamics due to increasing fire severity and stand mortality (Minnich 2001). The maintenance of standing forests (mixed-conifer forest, bigcone Douglas fir forest) with recurrent subcanopy fires may be compromised by increasing fire intervals (e.g., Swetnam 1993; Minnich et al. 2000), stand-densification (Minnich et al. 1995; Albright 1998; Roy and Vankat 1999) and increasingly extensive stand-replacement burns. Over long time scales, the transformation of these forests from "standing" population dynamics to either "shifting" or "patch mosaic" dynamics may result in progressive regional extirpations, a trend seen in the 20th century.

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SALTUGILIA LATIMERI: A NEW SPECIES OF POLEMONIACEAE

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Abstract

Saltugilia latimeri, a new species of Polemoniaceae, is endemic to dry, rocky to sandy slopes and foothills, primarily in San Bernardino and Riverside Counties, California. *Saltugilia latimeri* superficially resembles *S. australis* and has, until now, been considered conspecific with this taxon based on the small corolla size shared by both species. The two species differ in several morphological characters including stature, corolla throat coloration and exertion, and degree of glandularity.

Saltugilia latimeri, species, Polemoniaceae, taxonomy

Gilia is the historical catchall genus within Polemoniaceae for species of uncertain phylogenetic affinity (Wherry 1940, Mason and Grant 1948). Within this polyphyletic genus, Mason and Grant (1948) described a new taxon, *Gilia splendens* ssp. *australis* H. Mason & A. D. Grant, with stamen insertion and corolla throat and tube proportions similar to those of *Gilia splendens* H. Mason & A. D. Grant, but with a smaller corolla and a proportionally longer limb, similar in these respects to *Gilia caruifolia* Abrams.

As characters delimiting putative natural groups within *Gilia* were identified, such groups have been recognized with sectional or generic status. In one such case, Grant and Grant (1954) constructed *Gilia* section *Saltugilia* and included therein five species divided into two species groups. The section was considered to be natural from observations of corolla morphology and ecology of the members. Within their newly erected section *Saltugilia,* Grant and Grant (1954) elevated *G. splendens* ssp. *australis* to the species level, as *Gilia australis* (H. Mason & A. D. Grant) V. E. Grant & A. D. Grant. Grant and Grant (1954) distinguished *G. australis* from *G. splendens* and *G. caruifolia* by its smaller stature, whitish flowers (pale violet to white), and simpler leaves. The authors also noted minimal geographic overlap, partial to full breeding barriers, and apparent ecological isolation between *G. australis* and these other species.

Johnson (in Porter and Johnson 2000) elevated *Saltugilia* to generic status within Polemoniaceae. Following rules of priority, Porter and Johnson also restored Brand's (1907) epithet, *grinnellii,* in place of the more recently used epithet, *splendens,* for the largest-flowered species. As circumscribed by Porter and Johnson (2000), the genus *Saltugilia* comprises four closely related taxa: *Saltugilia australis* (H. Mason & A. D. Grant) L. A. Johnson, *S. caruifolia* (Abrams) L. A. Johnson, *S. grinnellii* (Brand) L. A. Johnson subspecies *grinnellii* and *S. grinnellii* subspecies *grantii* (Brand) L. A. Johnson.

A fifth taxon in *Saltugilia* has been identified. Our observations of greenhouse-grown plants and herbarium specimens indicate that two distinct forms have been referred to *S. australis* (as *Gilia australis*). Herbarium collections at RSA indicate that Latimer (1958) recognized, in his unpublished dissertation, these two forms as distinct subspecies within *G. australis*: a typical subspecies *australis,* and a geographically restricted subspecies *desertorum.* Based on observations of additional distinguishing characters, we here describe this geographically restricted taxon as a new species in the genus *Saltugilia.*

Saltugilia latimeri T. L. Weese & L. A. Johnson, sp. nov. (Fig. 1)—TYPE HERE DESIGNATED: USA, California, Riverside County, canyon in pass between Whitewater and Morongo Valley, 0.4 miles south of the San Bernardino county line, 9 April 1950, Verne & Alva Grant 8840 (holotype, RSA!).

Species nova ab *Saltugilia australis* (H. Mason & A.D. Grant) L.A. Johnson differt tubo corollae violaceo et exserto (nec albo et incluso), lobi corollae acutis (nec cuspidatis), et calyce dense glanduloso (nec glabro, glabrescenti, vel sparse glanduloso).

Annual herbs, to 30 cm in height, scapiform with a central stem and several basally branching axes subequal to equal with the main axis. Lower stems with long, uniserriate transparent trichomes commonly terminating in transparent glands (Fig. 1I; stalk cells becoming flattened and chain-like upon drying). Mid to upper stems densely glandular with the glands multicellular, flat-topped, and translucent (Fig. 1J; chloroplasts present in glands, but these neither darken beyond amber nor appear anthocyanic, as is common in *Gilia*). Lower leaves persistent, 5–many, forming a loose to dense basal rosette. Basal and lower cauline leaves generally 2×–3× pinnately divided with 3–10 sub-opposite lobes; leaf blade 20–45 mm long (–70 mm on greenhouse grown plants), 6–16 mm wide (–40 mm on greenhouse grown plants; Fig. 1C). Rosette and lower cauline leaves

with transparent, glandular trichomes of varying lengths (Fig. 1H). Upper cauline leaves glandular (Fig. 1K), reduced, bract-like, entire or occasionally pinnately divided, 1.5–14 mm long (–30 mm on greenhouse grown plants) and 0.2–6 mm wide (–17 mm on greenhouse grown plants; Fig. 1D). Inflorescence cymose, with flowers borne singly, or paired on ultimate stem extensions. Pedicels 2–16 mm long, occasionally longer, densely glandular (cf. Fig. 1L). When paired, pedicel of terminal (first maturing) flower usually shorter than pedicel of lateral (second maturing) flower (Fig. 1E). Calyx 2.6–3.5 mm long in flower, densely glandular (Fig. 1L–N), with an average of 20 glands per calyx lobe on herbarium sheets (range from 6 to 35 glands per calyx lobe). Calyx lobes dull green, sometimes purple spotted, 0.8 mm wide, united 3/5 length of calyx by an hyline membrane. Corolla 7.5–10 mm long, the fused portion 3–6.5 mm long, tube (=unexpanded portion of the fused corolla) exserted from the calyx. Tube dark lavender-purple, fading to blue (or yellow with extreme age) when dried. Lower throat (=expanded portion of fused corolla) yellow spotted; upper throat and lobes pinkish-lavender, but also fading to pale blue or yellowish on herbarium sheets. Corolla lobes 2.0–3.5 mm long and 1–3.5 mm wide, acute. Stamens inserted equally in the sinuses of the corolla lobes. Filaments 0.5–1.1 mm long to point of insertion, anthers 0.65–0.85 mm long and 0.35–0.50 mm wide. One stamen frequently extends at right angle to the throat. Style 7–8 mm long, extending slightly beyond the orifice. The three lobes of the stigma 0.8–1.0 mm long with tips curling downward. Capsule 3.5–5.0 mm long and 2.0–3.5 mm wide, typically 1.4–1.8 times as long as wide, more or less equaling the length of the calyx. Capsule dehiscent in three sections from the top to the base, 6–9 ovules per locule. Seeds ± 0.85 mm long, honey gold in color. Testa verrucate with anticlinal epidermal cell walls defined as low ridges, the ridges lost and cell wall boundaries obscure when this outer epidermal layer is shed upon wetting. Seeds mucilaginous via expansion of spericals when wet. Pollen grains blue, ±40 μm in diameter, 5–6 zonocolpate, with lirae radiating from the apertures in magnetic-field fashion. $n = 9$.

Paratypes. U.S.A. California, Inyo County: Hanaupah Cañon, Panamint Mountains, 16 May 1917, *Jepson 7091* (JEPS). Riverside County: Box Canyon, 16 Mar 1937, *Winblad s.n.* (CAS); Palms to Pines Hwy, Mount San Jacinto, 23 Apr 1937, *Winblad s.n.* (CAS); Palm Springs, 11 Apr. 1920, *Spencer 1569* (POM); Pinyon Flat, 1/2 way between Palm Canyon Drive and Jeraboa Road, 15 May 1992, *Johnson 92-021* (BRY, RSA, WS). San Bernardino County: Sandy-rocky place at base of foothills of Little San Bernardino Mountains, south of Yucca Valley, 6 May 1957, *Grant & Latimer 9986* (RSA); Cactus Flat, San Bernardino Mountains, 25 Jun 1926, *Munz 10514* (POM 96484 in part); Gran-

ite Mountains, Mojave Desert, 13 May 1939, *Jaeger s.n.* (CAS, POM); About 3 miles East of Joshua Tree off road to Twentynine Palms, 3 May 1964, *Thorne 33975* (RSA).

Comparative morphology and relationships. Until now, *Saltugilia latimeri* has been regarded as conspecific with *S. australis.* Both species possess small flowers, tend toward a smaller stature, and are ecologically disposed to drier habitats relative to *S. grinnellii* and *S. caruifolia.* Because convergence in these features may result from selection imposed by similar habitat types and available pollinators, they are not necessarily useful indicators of phylogenetic affinities or taxonomic boundaries. Flower size, in particular, has received disproportionate emphasis as an identification tool in *Saltugilia* (Day 1993). As a result, small flowered representatives of *S. caruifolia* and *S. grinnellii* have been misidentified as *S. australis* (e.g., CAS 627511, POM 48851). Similarly, it seems likely that *S. latimeri* has escaped previous delimitation by over reliance on flower size, to the exclusion of other characters that clearly distinguish *S. latimeri* from *S. australis.*

Beyond flower size, *S. latimeri* differs from *S. australis* in other floral features (Table 1). The corolla of *S. australis* is whitish overall. The lobes are cusped at the apex and may be suffused with pink or bluish-lavender, but the tube and throat (exclusive of the yellow spots, characteristic of *Saltugilia*) remain white. Furthermore, the tube is more or less included within the calyx, the throat flares widely, and the calyx is mostly glabrescent at maturity. These features are consistent with the type (UC!) and populations examined from throughout *S. australis'* range. In contrast, *S. latimeri* has saturated pink to lavender, tapering acute corolla lobes, a colored and more narrowly funnelform throat, a purple, exserted tube, and a more intensely glandular calyx, with the glands large and as abundant as on the pedicel.

Although corolla coloration provides a definitive means of distinguishing *S. latimeri* from *S. australis* on fresh and most herbarium specimens, color may fade from *Saltugilia* flowers over time and can be a less reliable diagnostic character on some herbarium specimens of extreme age. On living plants, flowers senesce quickly (1–2 days after opening, personal observation), and there is insufficient time for the distinctive coloration to fade while the flowers remain on the plant, thus identification of *S. latimeri* relative to *S. australis* is straightforward. When color has faded on herbarium specimens, the exserted tube, narrower throat, and glandular calyx are useful secondary characteristics for distinguishing between *S. latimeri* and *S. australis.*

Relative to other *Saltugilia, S. latimeri* is readily distinguished from *S. caruifolia* in stamen features (short filaments inserted in the sinus of the corolla lobes vs. long exserted stamens inserted mid-

Scale Bars
1 cm (C,D,S-W)
1 cm (A,B)
0.5 cm (E-G, R)
0.1 mm (H-L)
50 μm (M,N)
100 μm (O)
10 μm (P)
10 μm (Q)
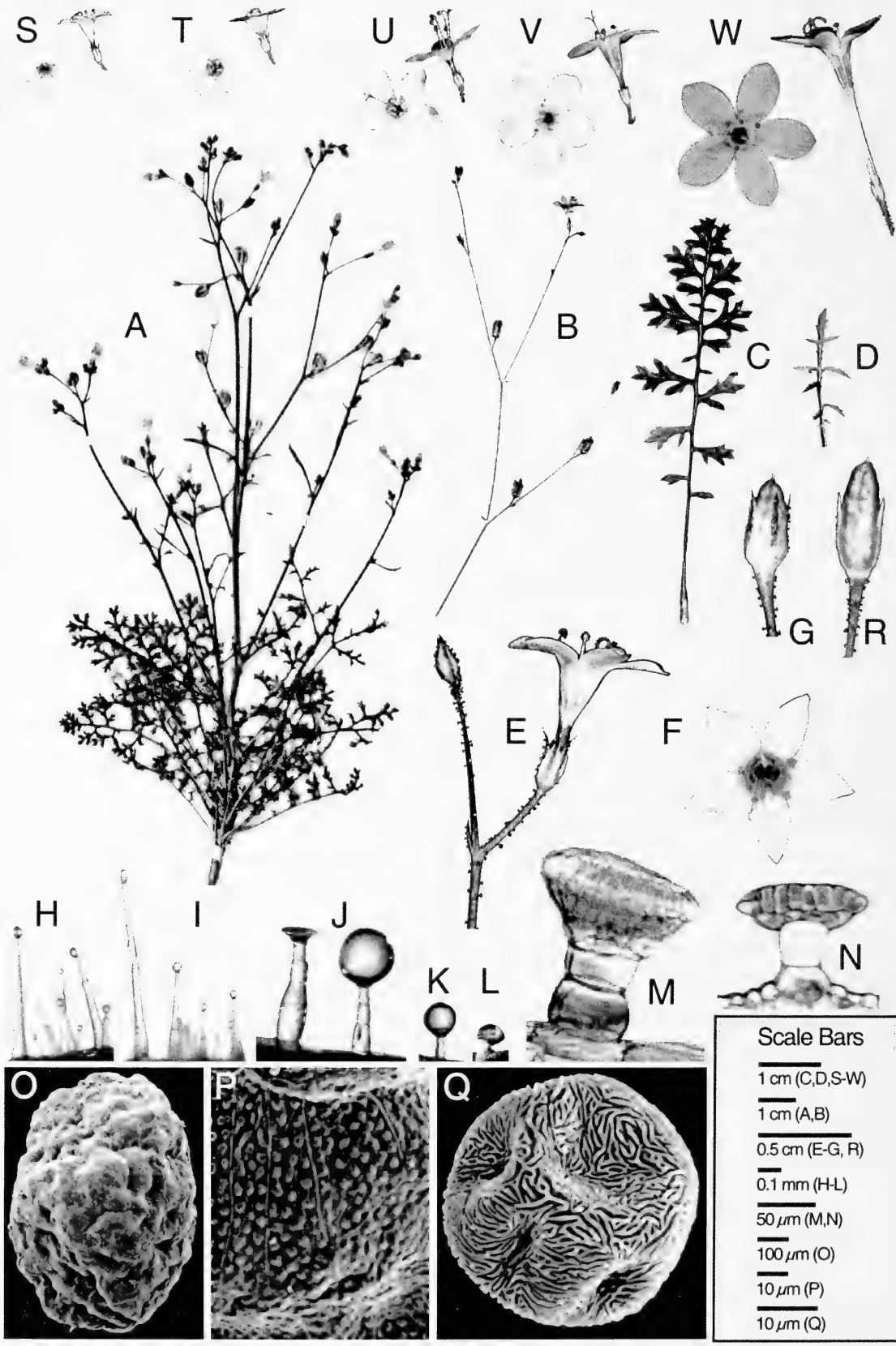
TABLE 1. MORPHOLOGICAL CHARACTERS OF *SALTUGILIA* SPECIES.

	Saltugilia australis	*Saltugilia caruifolia*	*Saltugilia grinnellii*	*Saltugilia latimeri*
corolla lobe color	white/pale pink	lavender/blue	lavender/bright pink	pink/lavender
throat color	white	white/lavender	lavender/pink	pink/lavender
tube color	white	purple	purple/pink	purple
petal lobe shape	cusped	obtuse/rounded	obtuse	acute, tapering
tube position relative to calyx	included	exserted	exserted	exserted
expansion of throat outside calyx	flares widely	wide flare/campanulate	narrow flare	narrow flare
stamen insertion	sinus of corolla lobes	mid throat	sinus of corolla lobes	sinus of corolla lobes
average number of glands per calyx lobe (min.–max. observed)	3 (0–7)	4 (0–11)	7 (0–27)	21 (6–35)
habit	one main central leader	one main central leader	one main central leader	branches near base

throat), and from *S. grinnellii* that tends to have rounder corolla lobe apices and a minutely glandular exterior corolla (Table 1). *Saltugilia latimeri* corollas most nearly approach the relative proportions of *S. grinnellii* corollas, although without the minute glands mentioned above.

As implied by morphology, *Saltugilia* are closely allied species differing primarily in corolla features. In addition to these floral characters, the capsule in *S. latimeri* is more or less equal to the calyx, whereas it frequently (but not always) greatly exceeds the calyx in *S. australis*. Differing from all other *Saltugilia*, *S. latimeri* also typically branches near the base so that several sub-equal lateral branches soon approach the central stem in length and diameter. In contrast, other *Saltugilia* usually have dominant central axes. Although the basal leaves of *S. latimeri* have broader, and fewer, lobe segments than typical *S. australis*, the leaves of *S. australis* show considerable variation across its range with some specimens possessing broader lobes.

Close relationships among *Saltugilia* species are also evidenced by hybridization studies. Grant and Grant (1954) concluded that species now placed in *Saltugilia* are interfertile, although these studies revealed that sterility to partial sterility exists between some populations (from 5 to 28% inviable individuals following interspecific crosses), leading Grant and Grant to hypothesize the presence of

semi-lethal gene combinations (see also Latimer 1958). Of relevance here, a cross between *S. latimeri* and *S. australis* produced viable F1 with pollen viability of 11% (Latimer 1958), compared to 58% viable pollen in F1 progeny of a cross between two populations of *S. latimeri*. This reduced fertility in interspecific crosses of *S. latimeri* × *S. australis* parallels our own results. A cross of *S. latimeri* (*Johnson 92-021*) with *S. australis* (*Johnson 92-011*, BRY) produced vigorous F1 offspring, but even hand pollination of the F1 produced only 1 to 7 seeds per capsule (average = 2.7; average number of ovules per capsule = 25) compared to an average of 23 seeds (24 ovules) and 19 seeds (21 ovules) in self pollinated capsules of the parental *S. latimeri* and *S. australis*, respectively. Pollen viability in hybrid progeny from other crosses reported by Grant and Grant (1954) averaged 14% between *S. caruifolia* and both subspecies of *S. grinnellii*, and 12% between extreme forms of the *S. grinnellii*. The ability of *S. latimeri* and *S. australis* to cross with *S. grinnellii* differed substantially (Latimer 1958). These hybridization studies provide inconclusive evidence regarding species boundaries and sister relationships within *Saltugilia*, but they do indicate levels of differentiation between *S. latimeri* and *S. australis* at least as great as between pair-wise combinations of other *Saltugilia* species.

Were *Saltugilia latimeri* itself the product of hy-

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FIG. 1. Features of *Saltugilia latimeri* alone and in comparison with selected features of other *Saltugilia*. A. habit in early flower. B. inflorescence branch in mid flower. C. basal leaf. D. cauline leaf. E, F. flower. G. capsule. H–L. trichomes from living plant. H. basal leaf. I. Lower stem. J. mid stem (gland on right with secretion present). K. flower bract (secretion present). L. calyx (secretion present). M. calyx gland cleared in choral hydrate. N. paraffin section of calyx gland. O. scanning electron micrograph of unhydrated seed. P. scanning electron micrograph of unhydrated seed surface showing verrucae and ridges formed from anticlinal walls. Q. scanning electron micrograph of untreated pollen grain. R. capsule of *S. australis*. S–W. relative size and shape of *Saltugilia* flowers. S. *S. latimeri*. T. *S. australis* (*Johnson 97-049*, BRY). U. *S. caruifolia* (*Johnson 97-099*, BRY). V. *S. grinnellii* subspecies *grinnellii* (*Johnson 93-098*, BRY). W. *S. grinnellii* subspecies *grantii* (Johnson 94-057, BRY). A, Q. *Grant & Grant 8840*, RSA. B-P, S. progeny of *Johnson 92-021*, BRY.

bridization, progeny of self-pollinated plants should demonstrate character segregation. In each generation, less intermediacy and more individuals with parental phenotypes would be observed. Four generations of greenhouse grown progeny from a single population have produced no segregation of morphological characters, supporting the autonomy of this species. Additionally, greenhouse grown plants readily set full capsules of seeds upon selfing, suggesting that *Saltugilia latimeri* is autogamous. Further evidence for autogamy is provided by allozyme analyses (26 individuals; *Johnson 92-021*) that reveal complete homozygosity at 28 surveyed putative loci representing 19 enzyme systems: AAT, ACN, ACPH, ALD, BGAL, CAT, EST, GDH, G3PDH-1, G3PDH-2, IDH, MDH-1, MDH-2, MDH-3, ME-1, ME-2, MNR-1, MNR-2, 6PGD-1, 6PGD-2, PGI−1, PGM-1, PGM-2, PGI-2, SKDH, SOD, TPI-1, TPI-2 (Following methods of Soltis et al. 1983 with or without minor modifications). Six of these 28 loci showed polymorphism with at most two alleles.

Sequences of the chloroplast *matK* region from *S. latimeri* (*Johnson 92-021*) have been included in molecular studies (as *Gilia australis*; Johnson and Soltis 1995, Johnson et al. 1996) and analyses of these data provide strong support for placing *S. latimeri* with other sampled representatives of *Saltugilia*. Additional sampling of multiple populations of all *Saltugilia* taxa (Weese and Johnson unpublished data) with sequences of the chloroplast *trnL* intron–*trnF* spacer and nuclear ITS regions strongly support the monophyly of *Saltugilia*, but provide insufficient resolution of taxa within the genus to use these markers alone as the basis of species recognition.

Grant and Grant (1954) proposed that species now included in *Saltugilia* evolved from an ancestral type, represented by *S. grinnellii* or a similar large flowered ancestor, occupying mild climatic conditions similar to those found along the California coast. Arising from this ancestral type were taxa adapted to extreme conditions, including the dry, arid habitats occupied by *S. australis*. This implies that *S. australis* represents an autogamous derivative from *S. grinnellii* or another similar large flowered ancestor. This hypothesis applies equally well to *S. latimeri*. We suggest *S. latimeri* represents a second, independent lineage of small-flowered, autogamous desert annuals derived from an ancestral *Saltugilia* species with features generally approaching those of *S. grinnellii*.

Ecology and distribution. Saltugilia latimeri grows in dry, desert slopes of coarse sandy to rocky soils at elevations of 400–1900 m. Flowering times typically range from mid April to early June, although collections have been made as early as mid March and as late as the end of June. Our survey of herbaria (CAS, JEPS, POM, RSA, SD, UCR, UC) reveals that fewer than 20 independent collec-

tions of *S. latimeri* exist. These were obtained from the Joshua Tree Wilderness Area at the border between San Bernardino and Riverside Counties, in the foothills of the Little San Bernardino, San Bernardino, and Santa Rosa Mountains, in the Granite Mountains of central San Bernardino County, and one disjunct collection in the Panamint Mountains of Inyo County (Fig. 2). This latter population is approximately 120 miles from other known *S. latimeri* populations.

Several collections of *S. latimeri* from the Granite Mountain range pose some taxonomic difficulty because they possess a central leader habit and cuspidate corolla lobes—two features typical of *S. australis*, but not characteristic of the holotype and paratypes listed above for *S. latimeri*. However, these collections fall within the limits of *S. latimeri* and can be identified based on their exserted, purple corolla tube, narrow corolla throat, capsule that is subequal to the calyx, and propensity for glandular calyces. The Granite and adjacent Old Dad Mountains (Fig. 2) represent a locality for *Saltugilia* separated by 50 miles from the nearest portion of *Saltugilia's* range in the desert slopes of the San Bernardino and Santa Rosa Mountains. Specimens referred to as *S. grinnellii, S. australis,* and *S. latimeri* have all been collected in the Granite Mountains, but only infrequently. Further study of this material, including new accessions, is warranted. The presence of these minimally intermediate *S. latimeri* collections in a geographically restricted location in no way interferes with the ability to differentiate *S. latimeri* from *S. australis* in other portions of these species' ranges. In addition to the Granite Mountain area, *S. latimeri* is in close proximity to *S. australis* in the Santa Ana and Little San Bernardino Mountains, and with *S. grinnellii* in the Morongo Canyon area of the Little San Bernardino Mountains (Fig. 2). Mixed collections of *S. latimeri* with other *Saltugilia* on herbarium sheets have not been observed.

Inferred from the small number of specimens present among *Saltugilia* collections acquired from seven herbaria (CAS, JEPS, POM, RSA, SD, UCR, UC), *S. latimeri* may merit conservation concern. Though almost certainly restricted in distribution, it is not known whether this species is truly rare or simply overlooked by collectors because of its small stature, inconspicuous habit, and short flowering duration. The habitat of *S. latimeri* includes desert scrub and chaparral communities that can be dense and difficult to navigate, perhaps leading to under-representation of this species in herbaria. However, more extensive collections of *S. australis* are available in several of these same areas, suggesting that *S. latimeri* is less abundant in nature. With human development encroaching in some of the known locations for this species, further study is warranted to establish the rarity of *S. latimeri*.

Whereas *S. australis* is frequently collected on first year burns within its range and its seeds re-
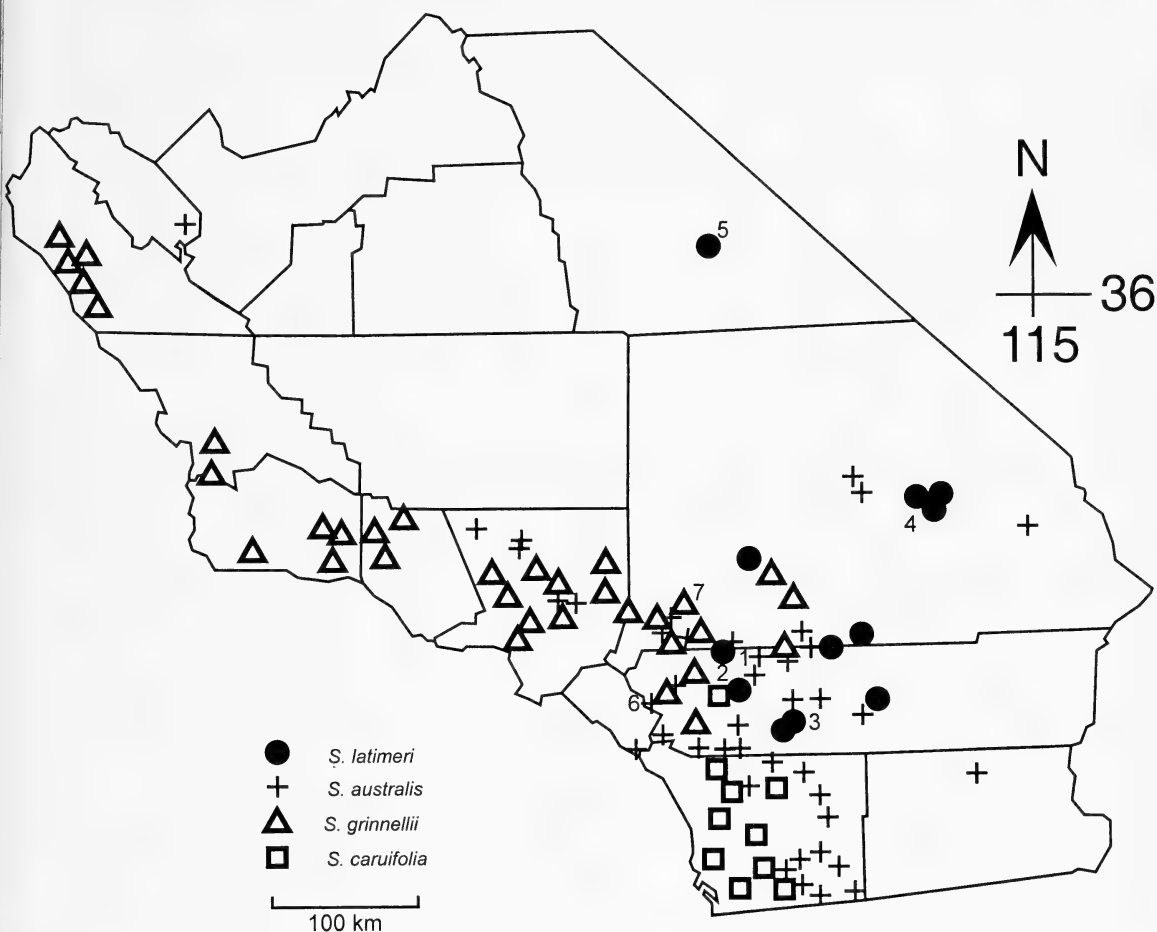
FIG. 2.   Distribution of *Saltugilia* species in California, USA. The ranges of *Saltugilia australis* and *S. caruifolia* extend into Baja Mexico, but these populations are not shown. Populations are represented by symbols: ● *Saltugilia latimeri*. + *Saltugilia australis*. △ *Saltugilia grinnellii*. □ *Saltugilia caruifolia*. Locations mentioned in the text are indicated by numbers: 1. Little San Bernardino Mountains. 2. San Bernardino Mountains. 3. Santa Rosa Mountains. 4. Old Dad/Granite Mountains. 5. Panamint Mountains. 6. Santa Ana Mountains. 7. Cushenbury Grade.

spond positively to charcoal as a germination cue (Keeley and Keeley 1987), no mention of fire is made on any specimen labels for *S. latimeri*. We routinely add charcoal when germinating seeds of all *Saltugilia* with great success, but have not rigorously determined whether *S. latimeri* responds more positively to this treatment than it would without the addition of charcoal.

Taxonomic evaluation of earlier studies. Because *Saltugilia latimeri* previously has not been distinguished from *S. australis,* earlier literature may include either of these species under the name "*Gilia australis*". Johnson and Soltis (1995) and Johnson et al. (1996) both include, as *Gilia australis* (*Johnson 92-021*), a population of *S. latimeri* in comparative DNA sequencing studies of the chloroplast *matK* gene. In both studies, *Saltugilia* is incompletely sampled (represented by *S. latimeri, S. caruifolia* and *S. grinnellii* ssp. *grantii* in Johnson and Soltis 1995 and *S. latimeri* and *S. grinnellii* ssp.

grantii in Johnson et al. 1996), yet forms a well-supported clade distinct from *Gilia.*

In their initial circumscription of *Gilia* section *Saltugilia,* Grant and Grant (1954) performed chromosome counts as well as extensive crossing studies within and among species of *Saltugilia.* The population of *G. australis* collected by Grant from Morongo Canyon in the San Bernardino Mountains (Fig. 2) used for these studies, and cited by Grant (1956), is *S. latimeri.* Additionally, specimens cited under the description of *G. australis* by Grant and Grant (1954) include both *S. australis* and *S. latimeri.* This is significant because the "desert race" of *Gilia splendens* discussed by Grant and Grant (1965) could be misconstrued to be our *S. latimeri.* This clearly is not the case, however, because this desert race of *G. splendens* is also discussed in Grant and Grant (1954), Latimer (1958) and Grant (1966).

Latimer's (1958) unpublished thesis recognized

S. latimeri at the subspecies level (as *G. australis* ssp. *desertorum*). In Grant's (1966) citation of Latimer's work, the populations of *Gilia australis* considered sympatric with *G. splendens* (collected in the Morongo Valley and Cushenbury Grade of the San Bernardino Mountains) are in fact *S. latimeri,* while those populations considered allopatric with *G. splendens* (collected inthe Santa Ana Mountains and Cajon Pass) are *S. australis* (Fig. 2).

Based on these observations, the recognition of *Saltugilia latimeri* as a new species in Polemoniaceae is warranted. This recognition is a starting point for further species level studies of *Saltugilia latimeri* and larger scale investigations both within *Saltugilia* and Polemoniaceae. To facilitate the correct identification and incorporation of *S. latimeri* in future works, the following key is provided.

KEY TO GENUS *SALTUGILIA*
(BEGINNING WITH COUPLET 55 OF PORTER AND JOHNSON 2000)

1. Trichomes on basal leaves eglandular white arachniod (present at least in axils), or white geniculate, or translucent; if translucent, inflorescence glands long stalked, diameter of gland less than length of stalk and generally equally abundant on pedicel and calyx, or inflorescence trichomes including long hairs . . . . *Gilia*
1.′ Trichomes on basal leaves translucent, minutely gland tipped; inflorescence glands subsessile, diameter of gland > length of stalk, more abundant on pedicel than calyx; pedicels and calyx without long stalked hairs . . . . 2 *(Saltugilia)*
2. Corolla tube and throat white (throat yellow spotted), adaxial lobe surface white to white suffused with blue, lavender, or pink; corolla tube included in calyx, corolla lobes cuspidate . . . . . *S. australis*
2.′ Corolla tube and throat pigmented (magenta to pink to purple and throat yellow spotted), adaxial lobe surface saturated blue, lavender, or pink; corolla tube exserted from calyx, corolla lobes rounded to acute (cuspidate only in Granite Mountains of San Bernardino County, California, but then possessing pigmented and exserted corolla tube) 3
3. Stamens exserted well beyond the corolla lobes, inserted equally mid throat; corolla lobes often reflexed, throat widely flaring, nearly campanulate, with purple marks visible on the interior of the throat at the base of each corolla lobe *S. caruifolia*
3.′ Stamens less than or equal to corolla lobes, inserted equally in the sinus of the corolla lobes; corolla lobes not reflexed, throat narrowly flaring, lacking purple marks on interior of throat 4
4. Corolla less than 11 mm long, corolla lobes pale pink to lavender, tube purple; corolla tube eglandular and calyx glandular . . . .*S. latimeri*
4.′ Corolla generally more than 11 mm long, corolla lobes pale to bright pink, tube pink to magenta; corolla tube minutely glandular, calyx eglandular to glabrescent . . . . 5 *(S. grinnellii)*
5. Corolla tube 4–10 mm long, 1–2 × calyx . . . . subspecies *grinnellii*

5.′ Corolla tube 7–18 mm long, 2–5 × calyx . . . . subspecies *grantii*

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TAXONOMIC CHANGES AND A NEW SPECIES IN *LASTHENIA* SECT. *AMPHIACHAENIA* (COMPOSITAE: HELIANTHEAE SENSU LATO)

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Abstract

A molecular phylogenetic study of the goldfield genus *Lasthenia* has clarified the relationships among taxa in the group. It has become desirable to make taxonomic and nomenclatural changes in order to reflect the relationships. *Lasthenia* sect. *Amphiachaenia* is the correct name for *L.* sect. *Baeria sensu* Ornduff (1966). The section now comprises six species and subspecies.

In consequence of a molecular phylogenetic analysis of the goldfield genus *Lasthenia* (Chan 2000; Chan et al. 2001), it has become desirable to revise the taxonomy of *L.* sect. *Baeria sensu* Ornduff (1966) (see Table 1 for a summary) to reflect the relationships of taxa within. The study utilized DNA sequence data from the internal and external transcribed spacers of 18S–26S nuclear ribosomal DNA and the 3' *trn*K intron of chloroplast DNA from multiple populations of taxa in *L.* sect. *Baeria sensu* Ornduff (1966) and close relatives. Relationships shown by molecular data are supported by morphology, chromosome numbers, and flavonoid chemistry (Bohm et al. 1974; Ornduff et al. 1974).

Ornduff (1966) included *Burrielia hirsuta* in his circumscription of *L.* sect. *Baeria sensu* Ornduff (1966) and did not account for the earlier sectional name *Burrielia* DC. sect. *Amphiachaenia* Nutt. The older sectional name is used here:

Lasthenia Cass. sect. ***Amphiachaenia*** (Nutt.) R. Chan, *comb. nov.* ≡ *Burrielia* DC. sect. *Amphiachaenia* Nutt., Trans. Amer. Phil. Soc. n.s. 7: 381. 1841.—TYPE SPECIES: *Burrielia hirsuta* Nutt. = *Lasthenia gracilis* (DC.) Greene.

Baeria Fisch. & Mey., Index Sem Hort. Petrop. 2: 29. 1836; Linnaea 11(Litt. Ber.): 96. 1837. ≡ *Lasthenia* Cass. sect. *Baeria* (Fisch. & Mey.) Ornduff, Univ. Calif. Publ. Bot. 40: 56. 1966, nom. illegit.—TYPE SPECIES: *Baeria chrysostoma* Fisch. & Mey. = *Lasthenia californica* DC. ex Lindl.

Leaves entire. Involucres bell-shaped, depressed-hemispheric, hemispheric, or obconic. Phyllaries free. Disc florets 10–100+, corollas 5-lobed, floral pigments turning bright red in dilute alkali. Anther tips deltate or sublanceolate to subulate, broadened above the base. Cypselae pappose or epappose; pappi monomorphic. $2n = 16, 32, 48$.

Maximum parsimony analysis has yielded results

showing that *L.* sect. *Amphiachaenia* is monophyletic only with the inclusion of *L. leptalea* from *L.* sect. *Burrielia*. More importantly, this study shows that *L. californica* (*sensu* Johnson and Ornduff 1978 and *sensu* Ornduff 1993; both = *L. chrysostoma sensu* Ornduff 1966) is cryptically diverse and is resolved into two robustly supported clades. One clade includes *L. macrantha pro parte*; the other may be sister to all other members of *L.* sect. *Amphiachaenia*. Each clade can be morphologically diagnosed by pappus morphology (see Fig. 1) and has a partially distinct distribution. No other morphological characters were found that could reliably distinguish the two clades. Although Rajakaruna and Bohm (1999) concluded that two geographical races of *L. californica sensu* Ornduff (1993) correspond to two edaphically distinct groups, I found that members of both clades span the habitat types to which the edaphic races appear to be restricted (N. Rajakaruna pers. comm.). In light of this, I have recognized each clade of *L. californica sensu stricto* as different species in *L.* sect. *Amphiachaenia* and have included L. *leptalea* in the section.

The smallest clade comprising *L. macrantha* also includes one clade of *L. californica sensu* Ornduff (1993). *Lasthenia macrantha* subsp. *bakeri* and *L. macrantha* subsp. *macrantha* and this clade of *L. californica sensu* Ornduff (1993) form a monophyletic group with *L. macrantha* subsp. *prisca* emerging as sister to this robustly supported clade. These results support previous interpretations of a close relationship between *L. californica sensu* Ornduff (1993) and *L. macrantha*. Close relationship between these two species was first recognized by Gray (1857), who treated them as varieties of the same species. Ornduff (1966) discussed the relationships in detail and Ornduff (1971) stated that *L. californica* (*sensu* Ornduff 1993) "may be viewed as an annual version of *L. macrantha*."

The close relationship between a clade of *L. californica sensu* Ornduff (1993), *L. macrantha* subsp. *bakeri,* and *L. macrantha* subsp. *macrantha* should now be reflected in their taxonomy by treating these

TABLE 1. COMPARISON BETWEEN *LASTHENIA* SECTS. *BAERIA* AND *BURRIELIA* SENSU ORNDUFF (1966, 1971, 1993) AND THE REVISED TAXONOMY. Corresponding species and subspecies are shown on the same line. *—sect. *Amphiachaenia* is the correct name for sect. *Baeria sensu* Ornduff (1966). **—*L. gracilis* was previously recognized as part of *L. californica sensu* Ornduff (1966, 1993).

Lasthenia Cass. *sensu* Ornduff (1966, 1971, 1993)	*Lasthenia* Cass.
sect. *Baeria* (Fisch. & Mey.) Ornduff	sect. *Amphiachaenia* (DC.) R. Chan*
	L. gracilis (DC.) Greene**
L. californica DC. ex Lindl.	*L. californica* DC. ex Lindl.
L. macrantha (A. Gray) Greene	subsp. *californica*
subsp. *macrantha*	subsp. *macrantha* (A. Gray) R. Chan
subsp. *bakeri* (J. T. Howell) Ornduff	subsp. *bakeri* (J. T. Howell) R. Chan
subsp. *prisca* Ornduff	*L. ornduffii* R. Chan
sect. *Burrielia* (DC.) Ornduff	
L. leptalea (A. Gray) Ornduff	*L. leptalea* (A. Gray) Ornduff
	sect. *Burrielia* (DC.) Ornduff
L. debilis (Greene ex A. Gray) Ornduff	*L. debilis* (Greene ex A. Gray) Ornduff
L. microglossa (DC.) Greene	*L. microglossa* (DC.) Greene

three taxa as members of *L. californica sensu stricto*. I am provisionally continuing to recognize these three taxa (as subspecies) pending further studies to assess relationships in the clade. The molecular results, coupled with differences in morphology (D. Keil pers. comm.) also suggest that *L. macrantha* subsp. *bakeri* and *L. macrantha* subsp. *macrantha* populations at the southernmost parts of their ranges may warrant treatment as distinct taxa in their own right.

I have assigned *L. macrantha* subsp. *prisca* to species rank as *L. ornduffii* based on chromosomal, morphological, biogeographical, physiological, and molecular evidence (Chan 2000; Chan et al. 2001; Ornduff 1971). *Lasthenia macrantha* subsp. *prisca* is a tetraploid Oregonian endemic with fleshy roots and narrower leaves compared to the hexaploid Californian subspecies with tap roots and broader leaves. Ornduff (1966) also reported that the Oregon populations of *L. macrantha* are long-lived pe-
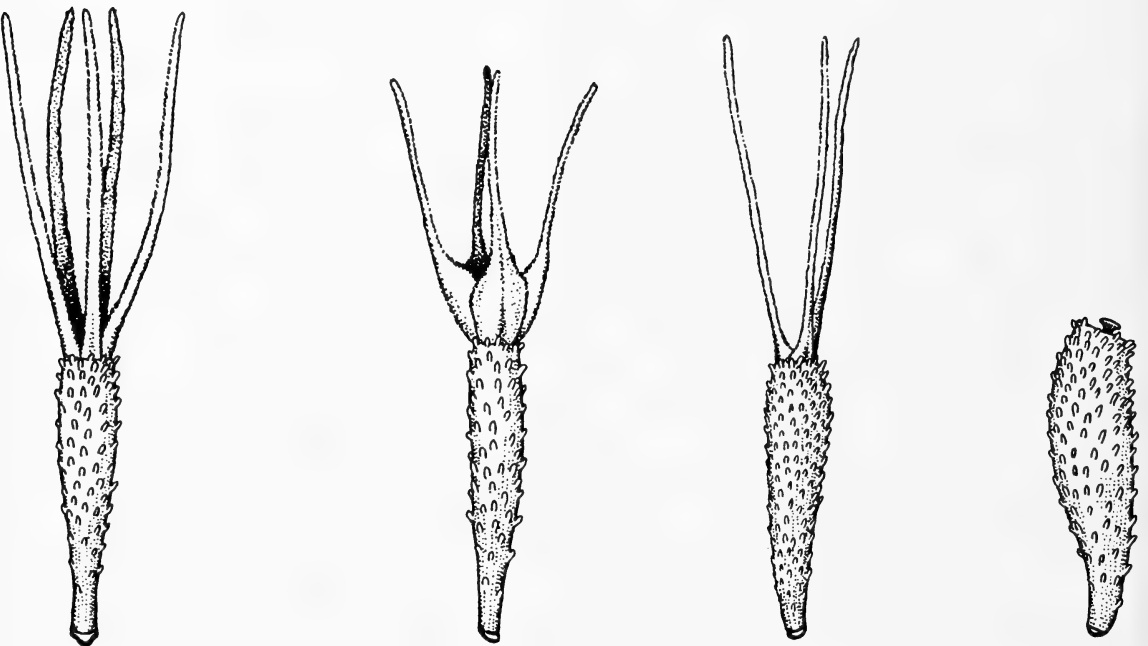
FIG. 1. Different pappus types present in *L. californica* subsp. *californica* and *L. gracilis*. A—clear to brown linear awns (*L. californica* subsp. *californica* only); B—opaque, white, ovate-lanceolate scales, each tapering to an awn (*L. gracilis* only); C—clear to brown subulate awns (*L. californica* subsp. *californica* only); D—epappose (both *L. californica* subsp. *californica* and *L. gracilis*). Dimensions are given in descriptions in the text.

rennials whereas their Californian counterparts may flower during the first year and behave as annuals under prolonged drought conditions.

KEY TO *LASTHENIA* SECT. *AMPHIACHAENIA*

1. Plants annual; coastal or inland.
  2. Stems glabrous proximally; receptacles narrowly conic; phyllaries usually 3–6, glabrous except at tips; anther tips subulate; interior western California (Monterey and San Luis Obispo counties) . . . . 3. *L. leptalea*
  2. Stems pubescent; receptacles conical; phyllaries usually 6–13, pubescent; anther tips deltate; coastal or inland.
    3. Pappi, when present, of 1–7, clear to brown, linear to subulate awns (see Figs. 1A and 1C); northern California and Oregon . . . . 1a. *L. californica* subsp. *californica*
    3. Pappi, when present, of (2–)4(–6) opaque, white, ovate-lanceolate scales, each tapering to an awn (see Fig. 1B); California (including the Channel Islands), central Arizona, and Baja California (including Guadalupe Island) . . . . 2. *L. gracilis*
1. Plants perennial; coastal.
  4. Roots fleshy, clustered; stems erect, 0–2+-branched; leaves usually 1–2 mm wide; California . . . . 1b. *L. californica* subsp. *bakeri*
  4. Roots not fleshy, not clustered; stems decumbent, usually 0–5+-branched at base; leaves usually 2–5.5 mm wide; California or Oregon.
    5. Leaves 28–88 mm long; laminae of ray corollas 6–18 mm long; California . . . . 1c. *L. californica* subsp. *macrantha*
    5. Leaves usually 20–40 mm long; laminae of ray corollas 5–9 mm long; southern Oregon . . . . 4. *L. ornduffii*

1. **Lasthenia californica** DC. ex Lindl., Edwards's Bot. Reg. 21: facing pl. 1780. 1835.—TYPE: "HHS [Hort. Horticultural Society of London]," grown in London from seeds collected in California by David Douglas, *J. Lindley s.n.* (holotype: CGE!).

Plants annual or perennial, 5–40 cm. Roots fibrous, from taproot or fleshy, clustered. Stems erect or decumbent, simple or 1–5(–20+)-branched, ± pubescent or hirsute. Leaves linear to oblanceolate, 8–210 mm long, 1–5.5(–15) mm wide, entire or with 3–5+ short, lateral teeth, ± fleshy in coastal forms, glabrous or sparsely to densely pubescent, or ± hirsute. Involucres bell-shaped, depressed-hemispheric, or hemispheric. Phyllaries 4–16, 5–14 mm long, pubescent. Receptacles conic, muricate, usually glabrous. Ray florets 6–16, laminae of ray corollas 5–18 mm long. Anther tips deltate to sublanceolate. Style tips deltate with apical tufts of hairs and subapical fringe of shorter hairs. Cypselae linear to ± club-shaped, 2–4 mm long, glabrous or pubescent, pappose or epappose; pappi of 1–7, clear to brown, linear to subulate awns. $2n = 16$, 32, 48.

1a. **Lasthenia californica** DC. ex Lindl. subsp. **californica**

Baeria chrysostoma Fisch. & Mey., Index Sem. Hort. Petrop. 2: 29. 1836; Linnaea 11(Litt. Ber.): 96. 1837. ≡ *Burrielia chrysostoma* (Fisch. & Mey.) Torr. & A. Gray, Fl. N. Amer. 2: 379 1842. ≡ *Lasthenia chrysostoma* (Fisch. & Mey.) Greene, Man. Bot. San Francisco 205. 1894.—LECTOTYPE (Ornduff, 1966, p. 57): California, Sonoma Co., vicinity of present-day Fort Ross, protologue: "Hab. circa coloniam Ruthenorum Ross, in sinu Bodega, Nova California," 1832, collector unknown (L; isolectotype: BM!).
Baeria gracilis A. Gray var. *aristosa* A. Gray, Proc. Amer. Acad. Arts 19: 21. 1883. ≡ *Baeria aristosa* (A. Gray) Howell, Fl. N. W. Amer. 1: 354. 1900.—TYPE: illustration in Bot. Mag. 66(13 n.s.): pl. 3758. 1840.
Lasthenia hirsutula Greene, Man. Bot. San Francisco 206. 1894. ≡ *Baeria hirsutula* (Greene) Greene, Fl. Fran. 438. 1897. ≡ *Baeria chrysostoma* Fisch. & Mey. subsp. *hirsutula* (Greene) Ferris, Contr. Dudley Herb. 5: 99. 1958.—LECTOTYPE (Ornduff, 1966, p. 57): California, Monterey Co., Pt. Lobos, protologue: "Along the seacoast from Marin Co. southward," 1 Jul 1891, *E. L. Greene s.n.* (ND!).

Plants annual. Roots fibrous, from taproot. Stems erect or decumbent, simple or 1–6(–10+)-branched, ± hirsute. Leaves 8–70 mm long, 1–3 mm wide, ± hirsute. Involucres bell-shaped or hemispheric. Phyllaries 4–13, 5–10 mm long. Ray florets 6–13, laminae of ray corollas 5–10 mm long. Anther tips deltate. Style tips deltate with apical tufts of hairs and subapical fringe of shorter hairs. Cypselae ± club-shaped, 2–3 mm long, glabrous or pubescent, pappose or epappose; pappi of 1–7, clear to brown, linear to subulate awns. $2n = 16$, 32, 48.

Lasthenia californica subsp. *californica* grows in a variety of habitats in southwestern Oregon and northern California. Within California, *L. californica* subsp. *californica* is found from northern Monterey, Santa Clara, Merced, and Madera counties northwards. *Lasthenia californica* subsp. *californica* was previously circumscribed together with *L. gracilis* as *L. californica sensu* Ornduff (1993). *Lasthenia californica* subsp. *californica* is morphologically very similar to *L. gracilis* but it can be distinguished from *L. gracilis* by its clear to brown, linear to subulate pappus awns (see Fig. 1A and 1C) and more northern distribution. In sympatric populations, epappose plants cannot be easily distinguished morphologically. Elevation 0–1,500 m. Flowering Feb–Jun.

Lasthenia hirsutula is a polyphyletic taxon comprising the maritime populations of *Baeria chrysostoma*. Plants matching the pappus morphology of both *L. californica* subsp. *californica* and *L. gracilis* are known to have been included in the

original circumscription of *L. hirsutula* (D. Keil pers. comm.). The type specimen of *L. hirsutula* possesses the pappus morphology of *L. californica* subsp. *californica* and is thus included here.

1b. **Lasthenia californica** DC. ex Lindl. subsp. **bakeri** (J. T. Howell) R. Chan, *comb. nov.* ≡ *Baeria bakeri* J. T. Howell, Leafl. W. Bot. 1: 7. 1932. ≡ *Baeria macrantha* (A. Gray) A. Gray var. *bakeri* (J. T. Howell) Keck, Aliso 4: 101. 1958. ≡ *Lasthenia macrantha* (A. Gray) A. Gray subsp. *bakeri* (J. T. Howell) Ornduff, Univ. Calif. Publ. Bot. 40: 62. 1966.—TYPE: California, Mendocino Co., Pt. Arena, protologue: "meadowy opening in the forest on the coastal plain, six miles south of Pt. Arena," 26 Jun 1931, *M. S. Baker 5283* (holotype: CAS; isotype: US).

Plants perennial (rarely annual or flowering first year). Roots fleshy, clustered. Stems erect, simple or 1–2(–4+)-branched, ± pubescent. Leaves 20–210 mm long, 1–2 mm wide, glabrous or sparsely to densely pubescent, basally clustered. Involucres bell-shaped to depressed-hemispheric. Phyllaries 13–16, 9–14 mm long. Ray florets 8–16, laminae of ray corollas 5–16 mm long. Anther tips deltate to sublanceolate. Style tips deltate with apical tufts of hairs and subapical fringe of shorter hairs. Cypselae linear to narrowly club-shaped, 2–4 mm long, usually glabrous, pappose or epappose; pappi of 1–4, clear to brown, subulate awns, variable or missing in some florets of a head. $2n = 48$.

Lasthenia californica subsp. *bakeri* grows in grasslands and woods along the coast in Mendocino and Sonoma counties. Populations of this rare subspecies appear to be increasingly more difficult to locate because of habitat destruction. Elevation 0–500 m. Flowering year round, mostly May–Jun.

1c. **Lasthenia californica** DC. ex Lindl. subsp. **macrantha** (A. Gray) R. Chan, *comb. nov.* ≡ *Burrielia chrysostoma* (Fisch. & Mey.) Torr. & A. Gray var. *macrantha* A. Gray in J. Torrey, Pacif. Railr. Rep. 4(5): 106. 1857. ≡ *Baeria macrantha* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 19: 21. 1883. ≡ *Lasthenia macrantha* (A. Gray) Greene, Man. Bot. San Francisco 205. 1894. ≡ *Baeria macrantha* (A. Gray) A. Gray var. *littoralis* Jeps., nom. illegit., Man. Fl. Pl. Calif. 1112. 1925.—TYPE: California, Marin Co., Pt. Reyes, protologue: "Punta de los Rey[e]s," Apr 1854, *Bigelow s.n.* (holotype: GH; isotypes: K, NY).

Baeria macrantha (A. Gray) A. Gray var. *pauciaristata* A. Gray, Proc. Amer. Acad. Arts 19: 21. 1883.—LECTOTYPE (Ornduff, 1966, p. 59): California, Mendocino Co., protologue: "sea shore," 4 Aug 1882, *C. G. Pringle s.n.* (GH; isolectotypes: K, NY).

Baeria macrantha (A. Gray) A. Gray var. *thalassophila* J. T. Howell, Leafl. W. Bot. 5: 108. 1948.—TYPE: California, Marin Co., Dillons Beach, protologue: "on ocean bluffs just above the high-tide line," 30 Apr 1947, *J. T. Howell 23108* (holotype: CAS; isotypes: UC!, US).

Plants perennial (rarely annual or flowering first year). Roots fibrous, from taproot. Stems usually decumbent, simple or 1–5(–20+)-branched at base, ± pubescent. Leaves 28–88 mm long, 1.5–5.5(–15) mm wide, glabrous to densely pubescent. Involucres bell-shaped to depressed-hemispheric. Phyllaries 9–16, 9–14 mm long. Ray florets 8–16, laminae of ray corollas 6–18 mm long. Anther tips deltate to sublanceolate. Style tips deltate with apical tufts of hairs and subapical fringe of shorter hairs. Cypselae linear to narrowly club-shaped, 2–4 mm long, usually glabrous, pappose or epappose; pappi of 1–4, clear to brown, subulate awns, variable or missing in some florets of a head. $2n = 48$.

Lasthenia californica subsp. *macrantha* grows in grasslands or on dunes along the immediate coast in Humboldt, Mendocino, Sonoma, Marin, San Mateo, and San Luis Obispo counties, California. *Lasthenia californica* subsp. *macrantha* is morphologically very similar to *L. ornduffii;* their ranges are allopatric. Elevation 0–500 m. Flowering year round, mostly May–Aug.

2. **Lasthenia gracilis** (DC.) Greene, Man. Bot. San Francisco 206. 1894. ≡ *Burrielia gracilis* DC., Prodr. 5: 664. 1836. ≡ *Baeria gracilis* (DC.) A. Gray, Proc. Amer. Acad. Arts 9: 196. 1874. ≡ *Baeria chrysostoma* Fisch. & Mey. var. *gracilis* (DC.) H. M. Hall, Univ. Calif. Publ. Bot. 3: 170. 1907. ≡ *Baeria chrysostoma* Fisch. & Mey. subsp. *gracilis* (DC.) Ferris, Contr. Dudley Herb. 5: 100. 1958.—TYPE: California, protologue: "In Nova-California legit cl. Douglas," *D. Douglas s.n.* (holotype: G!; isotypes: BM!, GH, K, NY).

Burrielia tenerrima DC., Prodr. 5: 664. 1836. ≡ *Baeria tenerrima* (DC.) A. Gray, Proc. Amer. Acad. Arts 9: 196. 1874. ≡ *Baeria gracilis* (DC.) A. Gray var. *tenerrima* (DC.) A. Gray, Syn. Fl. N. Amer. 1²: 326. 1884. ≡ *Baeria chrysostoma* Fisch. & Mey. f. *tenerrima* (DC.) H. M. Hall, Univ. Calif. Publ. Bot. 3: 171. 1907.—TYPE: California, protologue: "In Nova-California legit cl. Douglas," *D. Douglas s.n.* (holotype: G!; isotypes: BM!, K, NY).

Burrielia hirsuta Nutt., Trans. Amer. Phil. Soc. n.s. 7: 381. 1841.—TYPE: California, Santa Barbara Co., protologue: "Hab. Santa Barbara," *T. Nuttall s.n.* (holotype: BM!; isotype: GH).

Burrielia longifolia Nutt., Trans. Amer. Phil. Soc. n.s. 7: 380. 1841.—TYPE: California, Santa Barbara Co., protologue: "near Santa Barbara," *T. Nuttall s.n.* (holotype: BM!). [This specimen is also the type of *Baeria gracilis* (DC.) A. Gray var. *paleacea* A. Gray.]

Burrielia parviflora Nutt. Trans. Amer. Phil. Soc. n.s. 7: 381. 1841.—TYPE: California, Santa Barbara Co., protologue: "near Santa Barbara," *T.*

Nuttall s.n. (holotype: BM! [label states "St. Diego"]; isotypes: GH, NY).

Baeria palmeri A. Gray, Bot. Calif. 1: 376. 1876. ≡ *Baeria chrysostoma* Fisch. & Mey. var. *palmeri* (A. Gray) J. T. Howell, Leafl. W. Bot. 3: 152. 1942.—LECTOTYPE (Ornduff, 1966, p. 57): Mexico, Guadalupe Island, 1875, *E. Palmer 45* (PH; isolectotypes: BM, F, K, L, MBG, NY).

Baeria gracilis (DC.) A. Gray var. *paleacea* A. Gray, Proc. Amer. Acad. Arts 19: 21. 1883. ≡ *Baeria chrysostoma* Fisch. & Mey. f. *paleacea* (A. Gray) H. M. Hall, Univ. Calif. Publ. Bot. 3: 171. 1907.—LECTOTYPE (designated here): California, Santa Barbara Co., protologue: "near Santa Barbara," *T. Nuttall s.n.* (BM!). [This specimen is also the type of *Burrielia longifolia* Nutt.]

Baeria clevelandii A. Gray, Proc. Amer. Acad. Arts 19: 22. 1883.—TYPE: California, San Diego Co., protologue: "near San Diego," 1874, *D. Cleveland s.n.* (holotype: GH).

Baeria curta A. Gray, Proc. Amer. Acad. Arts 19: 21. 1883. ≡ *Baeria chrysostoma* Fisch. & Mey. f. *curta* (A. Gray) H. M. Hall, Univ. Calif. Bot. Publ. Bot. 3: 172. 1907.—LECTOTYPE (Ornduff, 1966, p. 57): California, San Bernardino Co., protologue: "near San Bernardino," 1880, *J. G. Lemmon 135,* (GH; isolectotype: UC!).

Baeria palmeri A. Gray var. *clementina* A. Gray, Syn. Fl. N. Amer. ed. 2, 1²: 452. 1886. ≡ *Baeria chrysostoma* Fisch. & Mey. f. *clementina* (A. Gray) H. M. Hall, Univ. Calif. Bot. Publ. Bot. 3: 172. 1907.—TYPE: California, San Clemente Island, 1885, *J. C. Nevin and D. Lyon s.n.* (holotype: GH; isotypes: DS, ND).

Baeria chrysostoma Fisch. & Mey. f. *nuda* H. M. Hall, Univ. Calif. Bot. Publ. Bot. 3: 170. 1907.—TYPE: California, Los Angeles Co., protologue: "San Francisquito Cañon," 3 May 1902, *H. M. Hall 3100* (UC!).

Baeria chrysostoma Fisch. & Mey. f. *crassa* H. M. Hall, Univ. Calif. Bot. Publ. Bot. 3: 172. 1907.—TYPE: California, San Diego Co., protologue: "Ocean Beach near San Diego," May 1906. *K. Brandegee* (holotype: UC!; isotypes: UC!, DS).

Plants annual, 5–40 cm. Roots fibrous, from taproot. Stems erect or decumbent, simple or 1–6(–10+)-branched, ± strigose. Leaves linear to oblanceolate, 8–70 mm long, 1–3 mm wide, entire or with 3–5+ short, lateral teeth, ± fleshy in coastal forms, glabrous or ± strigose. Involucres bell-shaped or hemispheric. Phyllaries 4–13, 5–10 mm long, ± strigose. Receptacles conic, muricate, glabrous. Ray florets 6–13, laminae of ray corollas 5–10 mm long. Anther tips deltate. Style tips deltate with apical tufts of hairs and subapical fringe of shorter hairs. Cypselae ± linear, 2–3 mm long, glabrous or pubescent, pappose or epappose; pappi of 2–6, usually 4, opaque, white, ovate-lanceolate scales, each tapering to an awn. $2n = 16, 32$.

Keck (1959) said of *L. gracilis* (as *Baeria chrysostoma* subsp. *gracilis*) "The most abundant composite in the state [of California]." It grows in a wide variety of soils and habitats throughout California, central Arizona, the Channel Islands, Guadalupe Island, and Baja California. It was circumscribed together with *L. californica* subsp. *californica* as *L. californica* by Ornduff (1993). It is morphologically very similar to *L. californica* subsp. *californica* and to *L. leptalea* but can be distinguished from *L. californica* subsp. *californica* and *L. leptalea* by its opaque, white, ovate-lanceolate scales, each tapering to an awn (see Fig. 1B). Elevation 0–1,500 m. Flowering Feb–Jun.

3. **Lasthenia leptalea** (A. Gray) Ornduff, Univ. Calif. Publ. Bot. 40: 63. 1966. ≡ *Burrielia leptalea* A. Gray, Proc. Amer. Acad. Arts 6: 546. 1865. ≡ *Baeria leptalea* (A. Gray) A. Gray, Syn. Fl. N. Amer. 1²: 325. 1884.—TYPE: California, Monterey Co., Santa Lucia Mountains, protologue: "on very dry hillside along the Nacisomento [Nacimiento] River," 2 May 1861, *W. H. Brewer 548* (holotype: GH; isotypes: K, UC!, US).

Plants annual, 5–15 cm. Roots fibrous, from taproot. Stems erect, simple or 1–5+-branched, glabrous proximally, densely villous in peduncular region. Leaves linear, 3–20 mm long, entire, sparsely pubescent. Involucres obconic to bell-shaped. Phyllaries 3–6, 4–6 mm long, glabrous but for pubescent tips. Receptacles narrowly conic, glabrous. Ray florets 6–9, laminae of ray corollas 2.5–5 mm long. Anthers tips subulate. Style tips ± deltate, with long apical pubescence. Cypselae linear to narrowly club-shaped, ca. 2 mm long, sparsely pubescent; pappi of 1–4, white to yellowish, narrowly tapered awns, missing in some florets of a head. $2n = 16$.

Lasthenia leptalea usually grows in open areas of oak woodlands, interior southern Monterey and northern San Luis Obispo counties, California. *Lasthenia leptalea* is morphologically very similar to *L. gracilis;* it can be consistently distinguished from *L. gracilis* by its subulate anther tips and phyllaries pubescent at the tips. Elevation 0–650 m. Flowering Feb–Apr.

4. **Lasthenia ornduffii** R. Chan, *sp. nov.* Based on: *Lasthenia macrantha* (A. Gray) Greene subsp. *prisca* Ornduff, Madroño 21: 96. 1971.—TYPE: Oregon, Curry Co., protologue: "very abundant on Cape Blanco," 16 Jul 1929, *L. F. Henderson 11400* (holotype: UC!; isotypes: ORE, PH).

Plants perennial (rarely annual or flowering first year), 5–40 cm. Roots fibrous, from taproot. Stems usually decumbent, 1–3+-branched at base, ± pubescent. Leaves linear to oblong, 20–40 mm long, 1.8–3 mm wide, glabrous or densely pubescent. Involucres bell-shaped to depressed-hemispheric.

Phyllaries 8–14, 9–14 mm long, pubescent. Receptacles conic, muricate, usually glabrous. Ray florets 8–15, laminae of ray corollas 5–9 mm long. Anther tips deltate to sublanceolate. Style tips deltate, hairtufted. Cypselae linear to narrowly club-shaped, 2.5–4 mm long, usually glabrous, pappose or epappose; pappi of 1–4, clear to brown, subulate awns, often variable or missing in some florets of a head. $2n = 32$.

Lasthenia ornduffii is known from six or so populations in grasslands along the immediate coast in Curry Co., southern Oregon. Elevation 0–500 m. Flowering year round, mostly May–Aug.

Lasthenia ornduffii was originally described as a tetraploid subspecies of *L. macrantha*. The species name is intended to honor the late Professor Emeritus Robert Ornduff, a native Oregonian, in appreciation of his outstanding contributions to our understanding of the evolution of *Lasthenia* and other groups in the California flora.

Excluded names (L. californica sensu Ornduff 1993):

Baeria punctata Greene ex C. F. Baker, W. Amer. Plants 2: 8. 1903, nom. nudum. Based on *C. F. Baker 2962*, Lakeport, Lake Co., California.

Baeria subcilata Greene ex C. F. Baker, W. Amer. Plants 2: 8. 1903, nom. nudum. Based on *C. F. Baker 2857*, Lake Merced, San Francisco Co., California.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

CASTILLEJA TENUIS (A. A. Heller) Chuang & Heckard (SCROPHULARIACEAE).—Ventura Co., headwaters of Little Mutau Creek, T6N R20W sec. 1, alt. 2042 m, 18 Jun 2000, in moist swales among *Pinus jeffreyi,* associated with *Deschampsia danthonioides, Lotus purshianus,* and *Scutellaria siphocampyloides.* R. Burgess and T. Burgess 3940 (JEPS, SBBG), det. M. Wetherwax (JEPS).

Previous knowledge. Known from Alaska south to the Klamath Mountains, Cascade Range, Klamath Range, and Sierra Nevada of California, and disjunctly in the San Bernardino and Palomar mountains of southern California (as *Orthocarpus hispidus* Benth. in P. A. Munz 1963, 1974).

Significance. First records for Ventura County and the western Transverse Ranges, representing a disjunction of ca. 140 km southwest of nearest known records in the Sierra Nevada (e.g., Bartolas Creek, Kern County, Twisselmann 12452, JEPS) and ca. 180 km west of nearest known records in the San Bernardino Mountains (e.g., east of Bluff Lake, Thorne et al. 47843, RSA, UC).

TRICHOSTEMA MICRANTHUM A. Gray (LAMIACEAE).— Ventura Co., near Cuddy Ranch, R. Hoffmann s.n., 21 Sep, 1927 (SBBG), det H. Lewis (LA); Mutau Road, ca. 1 mi south of junction with Lockwood Valley Road, T7N R21W sec. 17, alt. 1646 m., 14 July 2000, in dry vernal pool with *Epilobium densiflorum, Myosurus minimus,* and *Psilocarphus tenellus* var. *globiferus.* R. Burgess and T. Burgess 4025 (LA, SBBG), det. H. Lewis (LA), also collected by Steve Junak at Yellow Jacket Meadows approximately 3.5 km east of this site (S. Junak, personal communication); dry sandy floodplain, associated with *Mimulus pilosus, Iva axillaris* var. *robustior, Cardaria pubescens,* and *Salix exigua,* south side of Lockwood Valley Road, T8N R21W sec. 25, alt. 1494 m., 22 July 2000, R. Burgess and T. Burgess 4048 (LA, SBBG), det. Harlan Lewis (LA).

Previous knowledge. Known from margins of meadows, drying lakes, and meadows in the San Bernardino Mountains, and the mountains of Baja California del Norte (Munz 1963, 1974; Lewis, Brittonia 5:276–303. 1945).

Significance. First record for Ventura County and the western Transverse Ranges, representing a disjunction of ca. 180 km from nearest known sites in the San Bernardino Mountains (e.g., Big Bear Lake, H. Lewis 1689, LA).

SENECIO IONOPHYLLUS E. Greene.—Ventura Co., on north-facing, granitic slopes associated with *Pinus lambertiana, Galium jepsonii, Arabis repanda,* and *Hulsea vestita* ssp. *gabrielensis,* west flank of Seward Mountain, T6N R19W sec. 5, alt. 2027 m., R. Burgess and T. Burgess 3948 (SBBG), det. D. H. Wilken (SBBG).

Previous knowledge. Known from dry, rocky coniferous forests in the southern Sierra Nevada, San Gabriel, and San Bernardino mountains of California (Munz 1963, 1974).

Significance. First record for Ventura County and the western Transverse Ranges, a disjunction of ca. 100 km from nearest known sites in the San Gabriel Mountains (e.g., Kratka Ridge, R. Bacigalupi 6423, JEPS).

PYROLA ASARIFOLIA Michaux ssp. *asarifolia* (ERICACEAE).—On vernally moist, n-facing slope, associated with *Pinus lambertiana, Galium jepsonii, Arabis repanda*

Senecio ionophyllus, west flank of Seward Mountain, T6N R19W sec. 5, alt. 2072 m., R. Burgess and T. Burgess 3947 (SBBG), det. D. H. Wilken (SBBG).

Previous knowledge. Known from Asia, western North America from Alaska south to California, and northeastern North America.

Significance. First record for Ventura County and the western Transverse Ranges, representing a disjunction of ca. 190 km southwest of nearest known sites in the Sierra Nevada (e.g., Whitney Meadows, Tulare Co., Purpus in 1895, UC) and ca. 180 km west of nearest known sites in the San Bernardino Mountains (e.g., Vivian Creek, Munz 7593, RSA).

—RICK AND TRISHA BURGESS, Ventura County Flora Project, 221 Juneau Place, Oxnard, CA 93030.

MEXICO

SETARIA ARIZONICA Rominger (GRAMINEAE).—Baja California Sur, mpio. de La Paz, area del Borrego Cimarrón, Sierra "El Mechudo", cerca del Rancho Las Animas, 25 km al N de San Juan de la Costa. 24°42′N 110°42′W. Alt. 375 m. Veg. Matorral Xerofilo. 20 Oct 1996. *Reymundo Domínguez C. 1665* (HCIB, ARIZ, ASC).

Previous knowledge. Known only from Pima and Santa Cruz Cos., AZ, and Sonora, Mexico. The species was described by J. Rominger in his monograph of North American *Setaria* (Illinois Biol. Monogr. No 29, pp 66–68. 1962). The type is *L. N. Gooding 3754* from the Baboquivari Mts., Pima Co., AZ (Holotype ARIZ). Four other specimens are cited, all from Pima and Santa Cruz Cos., AZ.

The cited collections were named *S. liebmannii* E. Fourn., a species which is superficially very similiar. Rominger considered his new species to be rare. Subsequent to publishing his monograph, Rominger made a few collections, which did not alter the known range. Originally he stated that all collections were within a 100 mile radius of Nogales, but he cited no gatherings from Mexico. Apparently he intended the "radius of 100 miles" to refer to the United States only. In recent years I have observed the species to be common in the area of Brawley Wash, SW of Tucson. It is frequently growing in the shade of mesquites, as mentioned by Rominger in the protologue. I have also seen it in some abundance in the Buenos Aires National Wildlife Refuge, near Arivaca, Pima Co. Although not rare, as Rominger thought, the species is not often collected. Aside from gatherings by Rominger, and several by my wife and me, the ARIZ herbarium has only one recent collection from Pima County: *R. S. Felger 97-16,* from just north of Tucson. Two recent collections from Santa Cruz Co. are *L. J. Toolin 2262* and *T. R. Van Devender 91-951,* both from the Tumacacori Mts. As documentation of *S. arizonica* in Mexico, ARIZ has *Beetle M-6969, T. R. Van Devender 90-489, 91-654, 92-1081* and *94-700,* all from Sonora, the latter two some 500 km south of the US-Mexico border. Most collectors since Rominger have commented on the abundance of the species in the areas where they found it.

Significance. First record from the Baja California pen-

insula. The Domínguez collection also extends the known range of the species some 200 km farther south.

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ARIZONA

SETARIOPSIS AURICULATA (E. Fourn.) Scribner (GRAMINEAE).—Pima Co., Altar Valley, 26 km S of Robles Junction. In a broad sandy wash draining into Brawley Wash. Rather local on a north-facing shady bank with *Setaria arizonica* and *S. grisebachii.* Elev. 800 m. 23 Aug 1990. *J. R. REEDER & C. G. REEDER 8553* (ARIZ, US, CAS, TEX).

Previous knowledge. There is no publshed record of this genus occurring in Arizona—nor in the US. Mc Vaugh (Flora Novo-Galiciana, 1983) gives the range as: "B.C., Son., Chih., Sin., Nay., Gto., Jal., Col., Gro., Méx., Mor., Oax., Pue., S.L.P., Chis., Camp., Yuc.; Centr. Amer." At ARIZ there is a specimen with the following label data: *J. J. Thornber* s.n. (ARIZ-38003) Nogales, Arizona, among shrubs. 10–12 Sep 1930. It was originally named *Chaetochloa grisebachii* var. *ampla* Scribn. & Merr., but in 1958 J. M. Rominger annotated it (correctly) as *Setariopsis auriculata* (Fourn.) Scribner. I find no record that this was published by Rominger, and the name does not appear in Kearney & Peebles' Arizona Flora (Supplement 1960), nor in Lehr's Catalogue of the Flora of Arizona (1978). Although one finds the name in the key to *Setaria* and allied genera in Rominger's monograph of North American *Setaria* (Illinois Biol. Monogr. No. 29. 1962), the author makes no further mention of the genus.

Significance. *Setariopsis* was collected in Arizona in 1930, but this failed to get into literature on Arizona grasses. The 1990 collection reported here documents that *Setariopsis* is, indeed, a part of the Arizona flora. It is also the first published report of the genus from the US. Moreover, it occurs about 50 km north of the US-Mexico border. I have visited this site several times during the past decade, and can report that the population, although small, is thriving. It is interesting that among the several Sonoran specimens of this species at ARIZ, the one nearest to Arizona is *T. R. Van Devender* et al. s.n. [ARIZ] collected in Palm Canyon, SE of Magdalena some 75 km south of the International Border.

ALOPECURUS ARUNDINACEUS. Poir. (GRAMINEAE).—Coconino Co. N end of Mormon Lake in a marshy area. A common species here, with other grasses; strongly rhizomatous. Elev. 2200 m. 21 June 1995. *J. R. Reeder & C. G. Reeder 9309* (ARIZ, US, CAS). Same area, one of the dominant grasses in marshy ground; plants strongly rhizomatous; associated here with *Phalaris arundinacea* and *Poa pratensis.* 24 June 1998. *J. R. Reeder & C. G. Reeder 9675* (ARIZ, RSA).

Previous knowledge. This grass is a native of Eurasia. In Hitchcock's Manual (1951) it is not included in the key to *Alopecurus,* but at the end of the treatment for that genus one finds the name *Alopecurus arundinaceus* Poir., along with a short description. As reason for its inclusion in the Manual, there is the statement: "Adventive in hay meadows, Labrador; North Dakota; Eurasia." According to a map kindly provided by Mary Barkworth, this species is now established in all northern states west of, and including, the Dakotas. The most southern records, according to Barkworth, are Cache Co., Utah and Garfield Co., Colorado.

Significance. First record of the species from Arizona; also apparently the most southerly locality in which it is recorded as growing spontaneously in the U.S.A.

TRIDENS ALBESCENS (Vasey) Wooton & Standley (GRAMINEAE).—Pinal Co., a well-established local population in a riparian habitat in a tributary of the Santa Cruz River in the environs of Casa Grande—near the Mormon Batallion Monument on Hwy. 387, ca. 2 miles N of its jct. with Hwy. 84. Elev. 1400 ft. [325 m]. 21 Oct 1991. *Dan James* s.n. (ARIZ, US, CAS).

Same area. Many clumps in a shallow tributary of the Santa Cruz River. 26 June 1997. *J. R. & C. G. Reeder 9598* (ARIZ, ASU, NMCR). The James specimen was brought to the ARIZ Herbarium by Horace Miller.

Previous knowledge. Hitchcock's Manual (1951) gives the range as CO, KS, NM, OK, TX. The ARIZ herbarium has specimens grown in Tucson in Experimental grass gardens in 1936, 1938, and 1939, but no material from plants which were growing spontaneously in Arizona.

Significance. First record of this species for Arizona. Also, it constitutes a considerable range extension. Prior to the Arizona collections the most westerly records for *Tridens albescens* were Sandoval and Doña Ana counties in New Mexico. That this species is well established in at least one area in Arizona is attested to by the fact that it was recollected in the same location 6 years later.

BRACHIARIA PLATYPHYLLA (Munro ex Wright) Nash (GRAMINEAE).—Santa Cruz Co., San Rafael Valley, pond on Ki-He-Kah Ranch, T23S R17E, Sec. 11 SW¼. Common prostrate annual in mud. Elev. 4850 ft. [ca. 1500 m]. 24 Aug 1991. *T. R. & R. K. Van Devender et al 91-689* (ARIZ). Same location: Abundant with other weedy vegetation along margin of pond. 22 Sep 1992. *J. R. & C. G. Reeder 8930* (ARIZ, ASU, US). San Rafael Valley, ca. 3.5 km SSW of Canelo Pass in vicinity of Little Outfit Ranch. Charco in grassland with scattered oaks and manzanitas. Abundant *Marsilea, Heteranthera,* and weedy grasses surrounding the pond. Fairly common along the pond margin with other dense vegetation. Apparently grazed by cattle. Elev. 1550 m. 22 Sep 1992. *J. R. & C. G. Reeder 8929* (ARIZ, NMCR). The two localities cited above are separated by some 8 km.

Previous knowledge. A native species from Florida to TX, OK; Mex., Cuba. Easily distinguished from grasses with a similar inflorescence by the spikelet orientation, the first glume turned toward the rachis.

Significance. First record from Arizona. Previously not known W of Texas. NOTE: R. D. Webster [The Australian Paniceae (Poaceae). Stuttgart: J. Cramer 1987] argued that the traditional character of spikelet orientation (with lower glume turned toward, or away from the rachis) used to separate *Brachiaria* from *Urochloa* is unreliable and, moreover, of minor significance. He proposed restricting the genus *Brachiaria* to a single species, *B. erucaeformis* (Sm.) Griseb., and relegating other traditional members of the genus to *Urochloa.* This suggestion has some merit and has been adopted by some agrostologists. Following Webster, the name of the plant under discussion would be *Urochloa platyphylla* (Munro ex Wright) R. D. Webster. (For an explanation of the author citations for these binomials, see Kartesz & Ghandi in Phytologia 69(4):303. 1990).

UROCHLOA PANICOIDES P. Beauv. (GRAMINEAE).—Maricopa County, Phoenix, in horse pastureland west of lumberyard at Precision Components, Inc., 1820 S 35th Ave. (at Durango). Grass lies flat to ground, radiating from center, flowering stalks rising upward. Formerly (at least 5 yrs. ago) grazed by Chaolais cattle, originally from France via Mexico. Grass made sudden appearance after first discing of pasture. 24 June 1988. *D. J. PINKAVA 14365* (ARIZ, ASU, CAS, TEX, US)

Previous knowledge. A native of e and s Africa, India, and Pakistan, and now adventive in many localities in warmer parts of the world. It was not mentioned in Hitchcock's Manual (1951), and McVaugh (Flora Novo-Galiciana, 1983) commented that the two collections he cited were apparently the first records of the species in America. In the United States it has now been reported from several localities in Texas and also from New Mexico. It is an aggresive annual which is listed in the Federal Noxious Weed Act.

Significance. First record of *Urochloa panicoides* in Arizona; also first report of the species in the U.S.A. west of Doña Ana Co., NM.

SCLEROCHLOA DURA (L.) P. Beauv. (GRAMINEAE).— Maricopa Co., Phoenix, Encanto Golf Course. Thriving on the fairway, where it has persisted for two or three years. 1 May 1988. *Robert Lytle* s.n. (ARIZ, ASU, US).

Previous knowledge. A rather inconspicuous annual, native to southern Europe and the Middle East. Adventive in the U.S. in several scattered locations in western states, usually as a weed in lawns, golf courses, and roadsides. Reported from WA, OR, ID, CO, UT, NM, TX. Also known from CA see Hickman 1993, Jepson Manuel.

Significance. First record for Arizona.

ENNEAPOGON CENCHROIDES (Licht.) C. E. Hubbard (*GRAMINEAE*).—Pima County, Santa Catalina Mountains, Molino Basin, south side of road, elevation 4500 ft [1370 m]. September 1976. *E. Schmutz* s.n. (ARIZ); along Mt. Lemmon Hwy. in the Molino Basin area, common along the highway, elevation 1280 m, 22 September 1980. *J. R. Reeder & C. G. Reeder 7329* (ARIZ). Tucson Mountains, in sandy soil of Oeste Wash, Tucson Mountain Park; T14S R12E S13 NE¼, elevation 2650 ft. [800 m] 29 October 1989 *P. D. Jenkins 89-70* (ARIZ).

Previous Knowledge. This species is a native of the Old World. Renvoize (Kew Bull. 22:393–402. 1968), in his study of the genus, gives the range of *Enneapogon cenchroides* as: "From Sudan southwards to the Cape Province of South Africa; through Arabia to India; also on Ascension Island." I have been unable to find that it is anywhere recorded as growing spontaneously in the U.S.A. Moreover, I have no information regarding when, nor why, it became established in the Santa Catalina and Tucson Mountains of Arizona. The ARIZ Herbarium has several other collections from the southern Santa Catalina Mountains between 600 and 1400 m, the latest with the date 1999.

ENNEAPOGON CENCHROIDES is a robust annual, which can attain a height of a meter. Although the spikelets are similar to those of our native *E. desvauxii* P. Beauv., it is readily distinguished by its much coarser stems, and the larger, somewhat open inflorescence which is often as much as 20 cm or more in length. The plant is quite attractive and conspicuous when in flower.

Significance. Although it has been documented by specimens at ARIZ since 1976, curiously there seems to be no record in the literature that it is established anywhere in the United States.

—JOHN R. REEDER, Herbarium, University of Arizona, 113 Shantz Building, Tucson, AZ 85721.

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WASHINGTON

AMARANTHUS BLITUM L. (AMARANTHACEAE).—King Co., Juanita Beach Park, wet sandy shore of Lake Wash-

ington, T26N R5E S30, elev. 4 m, 5 Sep 1998, *Weinmann 42* (WTU); S shore of Lake Sammamish, mouth of Issaquah Cr., sand and gravel shore of small island and adjacent park beach, T24N R6E S17, elev. 8 m, 25 Aug 1999, *Zika 14131* (WTU); S shore of Lake Sammamish, mouth of Laughing Jacobs Cr., gravelly shore, with *Lythrum salicaria, Cyperus bipartitus,* T24N R6E S16, elev. 8 m, 7 Oct 1999, *Zika 14560, Jacobson & Weinmann* (WTU); Bellevue, N shore of Phantom Lake, damp gravel near lawn, with *Hypericum mutilum, Portulaca oleracea,* T24N R5E S2, elev. 75 m, 15 Oct 1999, *Zika 14604, & Weinmann* (WTU).

Previous knowledge. Guernsey pigweed is introduced from the Mediterranean, and found as a weed in eastern North America, west to Utah.

Significance. First report for Washington. This and the following taxa are all from the Seattle metropolitan area.

BALLOTA NIGRA L. subsp. *FOETIDA* (Vis.) Hayek (LAMIACEAE).—King Co., Seattle, weed in shade, Univ. of Washington campus, T25N R4E S16, elev. 25 m, 26 Oct 1999, *Zika 14655 & Jacobson* (WTU).

Previous knowledge. Black horehound is native to Europe, and adventive in eastern North America, west to Nebraska.

Significance. First report for Washington.

BRIZA MINOR L. (POACEAE).—Kitsap Co., Restoration Point, SE end of Bainbridge Is., Puget Sound, weed in meadow near golf course, with *Perideridia gairdneri, Hypochaeris radicata, Agrostis capillaris,* T24N R2E S12, elev. 4 m, 20 Aug 1999, *Zika 14085 & Jacobson* (WTU).

Previous knowledge. Little quaking grass is a common weed in the Willamette River valley of northern Oregon, 200 km to the south.

Significance. First report for Washington.

CAREX PENDULA Huds. (CYPERACEAE).—King Co., Washington Park arboretum, naturalized along small creek, with *Ranunculus repens, Equisetum telmateia,* T25N R4E S21, elev. 15 m, 11 Oct 1999, *Zika 14576* (MICH, WTU).

Previous knowledge. Pendulous sedge is native to Europe and occasionally planted as an ornamental in western Washington. Known as an adventive in the arboretum for the last decade.

Significance. First report as an escape from cultivation in Washington.

CAREX PROJECTA Mack. (CYPERACEAE).—King Co., near NE shore of Rattlesnake Lake, just above high water line, in partial shade, with *Malus fusca, Alnus rubra, Salix sitchensis, Phalaris,* T23N R8E S34, elev. 275 m, 26 Jul 1996, *Weinmann 30, 31* (WTU); same site, 29 Sep 1999, *Zika 14428 & Weinmann* (WTU).

Previous knowledge. Necklace sedge is native to eastern North America, west to Saskatchewan.

Significance. First record as an adventive in Washington.

CAREX SYLVATICA Huds. (CYPERACEAE).—King Co., SE end of Mercer Is., Lake Washington, Clarke Beach Park, weed along shaded, paved trail, with *Lapsana, Hedera, Carex deweyana, Acer macrophyllum,* T24N R5E S30, elev. 10 m, 13 June 1998, *Weinmann 35* (WTU); same site, 6 Oct 1999, *Zika 14523 & Weinmann* (WTU).

Previous knowledge. Wood sedge is native to Europe, and has been reported as an adventive in southern British Columbia and eastern North America.

Significance. First report for Washington.

CRASSULA TILLAEA Lest.-Garl. (CRASSULACEAE).— King Co., Shilshole Bay, Seattle waterfront, 0.7 km S of Meadow Point, common weed in gravel and bare ground,

with *Poa annua, P. pratensis, Aira caryophyllea,* T25N R3E S3, elev. 2 m, 8 May 1999, *Jacobson s.n.* (WTU); same site, 25 May 1999, *Zika 13758 & Jacobson* (WTU).

Previous knowledge. Mossy stonecrop is native to Europe and adventive on the west coast, N to Lane Co., OR, 370 km to the S.

Significance. First report for Washington.

CYPERUS ODORATUS L. (CYPERACEAE).—King Co., West Point, Seattle waterfront, weed in wetland, with *Mentha pulegium, Cyperus eragrostis,* T25N R3E S9, elev. 2 m, 20 Oct 1999, *Jacobson s.n.* (EIU, WTU).

Previous knowledge. Rusty flat sedge is a pantropical weed, and has been collected in Multnomah Co., OR, 200 km to the S.

Significance. First report for Washington.

DATURA WRIGHTII Regel (SOLANACEAE).—King Co., Queen Anne, Seattle, Queen Anne Ave. near Boston St., weed in gravel parking lot, T25N R3E S24, elev. 120 m, 20 Oct 1999, *Zika 14632 & Jacobson* (WTU).

Significance. First report for Washington.

ERAGROSTIS CURVULA (Schrad.) Nees (POACEAE).—King Co., S side of West Point, Seattle waterfront, disturbed ground near path, T25N R3E S16, elev. 3 m, 4 August 1999, *Jacobson s.n.* (WTU).

Previous knowledge. Weeping lovegrass is native to Africa, and has been collected as an adventive in Multnomah Co., OR, 200 km to the S.

Significance. First report for Washington. Known from the site since 1998, and increasing.

GEUM URBANUM L. (ROSACEAE).—King Co., Island Crest Park, Mercer Is., Lake Washington, shaded trailside, and in wetland below suspension bridge, with *Hedera, Geum macrophyllum,* T24N R5E S19, elev. 90 m, 6 Oct 1999, *Zika 14532 & Weinmann* (WTU); Seattle, Univ. of Washington campus, T25N R4E S16, elev. 25 m, 26 Oct 1999, *Zika 14659 & Jacobson* (WTU); Seattle, Interlaken Park, shaded roadside, T25N R4E S20, elev. 40 m, 7 Oct 1999, *Zika 14554* (WTU); Seattle, arboretum, common along paths, T25N R4E S21, elev. 20 m, 4 Sept 1998, *Zika 13544* (WTU); Seattle, Lakeview Park, Harrison Ridge, bare ground, partial shade, T25N R4E 27.

Previous knowledge. Wood avens is native to Europe, and was first observed in the arboretum in 1978. It has been known as a weed in Portland, OR, since 1993, 230 km to the south.

Significance. First report for Washington.

PARIETARIA JUDIACA L. (URTICACEAE).—King Co., Capitol Hill, Seattle, near Aloha St., weed in cracks in concrete, T25N R4E S28, elev. 110 m, 20 Oct 1999, *Zika 14629 & Jacobson* (WTU); Pigeon Point, Seattle, near 19th St., weed on shaded ground near concrete steps, from top of bluff to base of West Seattle Bridge, T24N R3E S13, elev. 15–45 m, 20 Oct 1999, *Zika 14633 & Jacobson* (WTU).

Previous knowledge. Pellitory-of-the-wall is native to Africa and Eurasia. It is weedy in coastal California, 1000 km to the south.

Significance. First report for Washington.

PARIETARIA OFFICINALIS L. (URTICACEAE).—King Co., Seattle, Univ. of Washington campus, T25N R4E S16, elev. 25 m, 26 Oct 1999, *Zika 14657 & Jacobson* (V, WTU).

Previous knowledge. Eastern pellitory-of-the-wall is native to central and southern Europe. Cultivated at the medicinal herb garden of the University, it is now an occasional weed in the area.

Significance. First report for Washington as an escape from cultivation.

POTENTILLA INCLINATA Vill. (ROSACEAE).—King Co., Seattle, Univ. of Washington campus, T25N R4E S16, elev. 25 m, 26 Oct 1999, *Zika 14651 & Jacobson* (WTU).

Previous knowledge. Cultivated in the medicinal herb garden at the University for a decade, and readily reseeding in adjacent areas. Removed from the gardens ca. 1990, but persisting as a rare weed in the area.

Significance. First report for Washington as an escape from cultivation.

SCROPHULARIA NODOSA L. (SCROPHULARIACEAE).—King Co., Seattle, Univ. of Washington campus, T25N R4E S16, elev. 25 m, 26 Oct 1999, *Zika 14666 & Jacobson* (WTU); Seattle, Good Sheperd Center, NE 50th St., waste ground, T25N R4E S8, elev. 90 m, 16 May 2000, *Zika 14983* (WTU).

Previous knowledge. Common figwort is native to Europe and cultivated in the medicinal herb garden at the University. Now an occasional weed in the area.

Significance. First report for Washington.

VERBASCUM PULVERULENTUM Vill. (SCROPHULARIACEAE).—King Co., Seattle, Washington Park arboretum, rare weed along path, with *Dactylis, Lapsana, Poa pratensis, Taraxacum,* T25N R4E S21, elev. 20 m, 15 Sep 1999, *Zika 14338 & Jacobson* (WTU); arboretum, adventive by storm grate, T25N R4E S21, elev. 25 m, 17 Nov 1999, *Zika 14739 & Jacobson* (WTU).

Previous knowledge. Hoary mullein is native to Europe, and has not been reported as a wild plant in our area.

Significance. First report for Washington.

VERBENA OFFICINALIS L. (VERBENACEAE).—Seattle, Univ. of Washington campus, weed on waste ground, T25N R4E S16, elev. 25 m, 26 Oct 1999, *Zika 14649 & Jacobson* (WTU).

Previous knowledge. Vervain is native to Europe, and has been reported as a weed on ballast in Multnomah Co., Oregon, 200 km to the south.

Significance. First report for Washington.

—ARTHUR L. JACOBSON, FREDERICK C. WEINMANN, and PETER F. ZIKA, Herbarium, Dept. of Botany, Box 355325, Univ. of Washington, Seattle, WA 98195-5325.

A TRIBUTE TO THE CONTRIBUTIONS OF PROFESSOR JACK MAJOR

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Jack Major, Professor Emeritus of Plant Ecology at the University of California, Davis (UCD), died 13 February 2001 in Davis at the age of 83. Professor Major had a profound impact on the direction of plant ecology in the United States during the second half of the 20th century. His contributions to ecologists and land managers in California are particularly important, and those contributions were highlighted by the editors of *Madrono* in a 1982 issue dedicated to him (Parsons 1982; Anonymous 1982).

Jack's academic home for most of his career was the UCD Botany Department, where he taught from 1955 until retirement in 1981. His spiritual home, however, was in the mountains: the Uinta Mountains of Utah, the Sierra Nevada of California, the Grand Tetons of Wyoming, the Brooks Range and the Juneau ice fields of Alaska, and the Himalayas of Nepal. This was the environment that he most often shared with graduate students and those undergraduates fortunate enough to take his plant ecology classes. He truly was the ideal scientist described by Poincare (1958), as someone who ". . . does not study Nature because it is useful to do so. He studies it because he takes pleasure in it . . . [and] because it is beautiful."

Jack was born 15 March 1917 in Salt Lake City, UT and completed high school there in 1935. He went on to Utah State Agricultural College (now Utah State University) and received a BS in Range Management in 1942. For the next several years he served in the Army's 10th Mountain Division, the justifiably famous unit of 1000 skiers and alpinists who trained hard in the mountain west before participating in the Italian campaign (Fig. 1). After the war, a number of men from that Division went on to become conservationists, ecologists, and leaders in the promotion of recreational skiing. Between 1946 and 1953, Jack attended graduate school at the University of California, Berkeley, obtaining a PhD in Soil Science under the direction of Professor Hans Jenny. During this time he also met and married Mary Cecil, thanks to an introduction from brother Ted who had met Mary by chance on a rock climbing expedition in the Grand Tetons. She, too, had a love for the mountains. Mountain landscapes and vegetation remained lifetime passions for both of them and for their sons, as celebrated in Paul Castelfranco's 1988 poem, "Voices of the mountains:"

I listened to voices/The innumerable voices/Of the mountains. . .
Voices of red lava pinnacles/Voices of grey granite boulders. . .
And up the ridge/Above the forest/Above the meadow/
Through lodgepole, hemlock/And timberline.
From the crest I could see/Vast basins of granite/
And blue silhouettes/
In the distance.../
I listened/To all these voices/To the one complex chorus/Of the mountain.

Jack was hired as a member of a young weed science group in the Botany Department at UCD (Fig. 2). His strong interest in the ecology of undisturbed mountain vegetation, however, conflicted with the weed group's focus on plants in agronomic, low-elevation settings. This habitat bias gradually distanced him from weed science, and a 1964 Fulbright Fellowship to Innsbruck, Austria was to cement a lifetime's focus on vegetation science.

He had a driving curiosity that made him an extensive reader of, and correspondent with, scientists who specialized in a wide range of topics, including those who wrote in other languages. As a result, he was far ahead of his time. For example, we have correspondence in 1948 between Jack and Sewal Wright, one of the major contributors to the synthesis of Darwinism and Mendelism. Wright responded to Major's query of how to determine the relative importance of multiple interacting factors that explain a plant community's distribution limits, by describing his own original statistical method, path analysis. Path analysis has only been used regularly in the ecological literature for the past dozen years, but it was part of Jack's education 40 years earlier. Another example: Inspired by his major professor's book (Jenny 1941), *The factors of soil formation,* he wrote a paper (Major 1951) that proposed to use differential equations to describe the sum of vegetation-environment relationships for any given plant community. Not for another quarter of a century, however, did any ecologist actually begin to *use* differential equations in models of plant communities.

Several aspects of the Jenny/Major approach may now appear to be naive. Today—instead of relating attributes of soils or vegetation directly to the factors of soil formation—a clear distinction between, processes and factors seems now to be the more productive way to go (Humphreys and Paton 1998). But we must remember that Major's 1951 paper was written in a pre-ordination era before adequate canonical multivariate techniques with permutation tests and computers were available to test his hypotheses.

One measure of Professor Major's vision and impact is the fact that several of his earliest papers are still cited today, in some cases more often now than originally. According to the ISI Web of Science, "A functional, factorial approach to plant ecology" has been cited 91 times in the past 25 years. His superb synthesis of the California flora, geology, and ecology ("Endemism and speciation

FIG. 2. Assistant Professor Jack Major in 1956 as a new faculty member at UC Davis while on a departmental field trip at Calaveras Big Trees State Park. Photo courtesy of Roman Gankin.

FIG. 1. Corporal Jack Major when a member of the 10th Mountain Divisiion, 1944. Photo courtesy of (then Sergeant) Don Bothwick.

in the California flora,'' Stebbins and Major 1963) has been cited 102 times in the same period, and his most-often cited paper, ''Buried viable seeds in California bunchgrass sites and their bearing on the definition of flora,'' (Major and Pytott 1956) has been cited 138 times, and is still being cited at the rate of seven times per year for the past 5 years. His work on primary succession following glacial retreat (Crocker and Major 1955) is a classic, cited and described in many textbooks nearly a half-century later (e.g., Barbour et al. 1999; Begon et al. 1996; Krebs 2001) and in recent reviews on succession (Wali 1999).

Jack was one of very few Americans to practice the phytosociological protocols widely used in Europe (and throughout the non-English-speaking world) for the sampling and classification of vegetation. Consequently, releve sampling and syntaxonomy were employed by most of Jack's students in their dissertations (e.g., Neilson 1961; Pemble 1970; Taylor 1976; Burke 1979; Benedict 1981). Jack's gentle leadership in pulling reluctant American ecologists across a then-narrow bridge of communication into the rest of the world, was without doubt of seminal help later to Robert Whittaker in the 1970s when his travels and publications widened that bridge. Only now—20–30 years after his students have finished their graduate degrees—are phytosociological papers becoming accepted and publishable in the US.

Professor Major was the opposite of a bandwag-

on scientist. He preferred to go in his own sense of an appropriate direction, even when he was so far ahead of others that few understood his choice or took the same route. Paul Castelfranco's 1991 poem, ''Epitaph,'' captures this aspect of his personality: ''And on his grave some kindly person wrote/Never did he jump on a bandwagon . . . /He preferred to walk.''

Throughout his career, Dr. Major was as well-known for his reviews of ecological books written in other languages as for his own research. The journal *Ecology* alone publshed 158 of his book reviews, most of them of works written in French, German, and Russian. These detailed reviews brought foreign news and ideas to the attention of otherwise ethnocentric and linguistically challenged American ecologists. In 1975 the Ecological Society of America gave him its first Distinguished Service Citation specifically for his his prodigious reviewing activity, judged to be an outstanding service to Society members. According to then-President Richard Miller (1975), ''Major's reviews have consistently pointed out gaps in our own knowledge of American ecosystems and have indicated directions for fruitful new research . . . [We] would be immeasurably poorer without his dedicated efforts.'' Unfortunately, his encyclopedic knowledge of the literature has only partially been preserved in his papers, reviews, and bibliographies (Major and Rejmanek 1988/9). Unfortunately, also, is the fact that this kind of selfless scholarly work is poorly rewarded by the usual academic promotion process. Dr. Major's tenure promotion was repeatedly delayed and finally achieved long after those who

FIG. 4.   Jack and Mary Major hiking in the Grand Tetons in 1992. Photo courtesy of Ted Major.

FIG. 3.   Jack Major crossing an Alaskan stream in 1982, on his way to visit the research area of (then student) Ann Odaz. Photo courtesy of Dr. Odaz.

understood the value of his work would have awarded it.

He was a gentleman scholar: learned but soft-spoken and modest to the point of self-effacement. If presented in conversation with an opinion contrary to his own, he was sincerely quizzical and would quite innocently ask why one thought that way, rather than offering a defensive or challenging counter-statement. In this manner, Jack made those around him feel equally learned. Even when he disagreed with them, his own contrary opinions were delivered so delicately and non-confrontationally (usually ending with his traditional phrase, "Is this alright?") that the recipients might not realize their logic had been shredded until reflecting on it some days later.

His forte in teaching was with small groups. His low-key manner was not well suited to large lecture sections or busloads of fieldtrip students. On hikes in the field, a student had to be self-motivated enough to keep up and crowd close around him while he pointed out species and talked of their indicator value. Those who hung back missed a great education. His method of teaching was So-

cratic, inviting questions and asking questions back, usually including his stock phrase, "Is this alright?" because he didn't want to lose anyone. His classes and his research interests were reflected in theses, dissertations, and publications: alpine plant communities (Burke 1979; Neilson 1961; Major and Taylor 1977, 1988), biogeography (Taylor 1977), California vegetation (Barbour and Major 1977, 1988), gradient analysis (Waring and Major 1964), plant ecophysiology (Macdonald 1981; Barry 1968), plant-soil relations (Myatt 1968), systematics (e.g., Gankin 1957), the history of ecological concepts (Major 1969), and vegetation change (VanKat 1970). He was mentor to more than 20 graduate students of his own and to many more via correspondence or by way of serving as a member on their thesis/ dissertation committees (Fig. 3).

We join his wife Mary and sons Paul, John, and James, and brother Ted in their sorrow at his physical absence among us now; but the memories of his delight in the high country remain with us (Fig. 4). A modified version of this memorium recently appeared in the Bulletin of the Ecological Society of America (Barbour et al. 2001).

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MARITIME CHAPARRAL COMMUNITY TRANSITION IN THE ABSENCE OF FIRE

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Abstract

Maritime chaparral stands on California's central coast are dominated by a number of endemic *Arctostaphylos* species and are the habitat for several other species of concern. Although chaparral is a fire-adapted vegetation type, maritime chaparral occurs in densely populated regions where fire suppression prevents most stands from burning. In 2000, we re-sampled vegetation at six locations in north Monterey County's Prunedale sandhills that were sampled in 1975–1976 by Griffin (1978); this allowed us to document changes in community composition, canopy cover, and seedling abundance over a 25-year interval after more than 70 years of fire exclusion. Although species richness in the tree and shrub layers changed little between 1975–1976 and 2000, combined tree and shrub cover increased from 86 to 99%. Cover of *Arctostaphylos pajaroensis* J. Adams increased from 58 to 82%. Cover of *Quercus agrifolia* Nee and *Heteromeles arbutifolia* (Lindley) Roemer also increased significantly, whereas percent cover for most shrub species decreased, often dramatically. Species richness in the herb layer was markedly lower in the 2000 survey. Seedlings were rare under the dense canopy, although seedling abundance for *Q. agrifolia* and *Mimulus aurantiacus* Curtis increased. These results suggest that the long absence of fire in maritime chaparral stands may lead to dominance by one or two species and a gradual transition from chaparral to oak woodland. Land managers should consider the reintroduction of wildfire, or practices that mimic the effects of fire, to assure the long-term survival of maritime chaparral vegetation communities.

Introduction

Large areas of California's central coast are reported to have been covered with dense chaparral at the end of the nineteenth century (Cooper 1922). Today, only small, isolated fragments of northern and central maritime chaparral can be found growing in well-drained sandy soils along ridgelines and on coastal terraces between Sonoma and Santa Barbara counties (Holland 1986). Each of these stands is dominated by one or more *Arctostaphylos* species, including about 20 that are narrowly distributed endemics (Hickman 1993).

Although chaparral is widely reported to be dependent on periodic burning for renewal (e.g., Wells 1962; Hanes 1988), the cool and foggy central coast has one of the lowest rates of lightning-caused fire in California (Greenlee and Langenheim 1990). Estimates of historic fire return intervals for the Monterey Bay area range from as short as 10 to as long as 100 years or more (Greenlee and Langenheim 1990; Moritz 1997), but none of these estimates are presented with much confidence. Modern fire suppression practices have greatly reduced the size and frequency of wildfires in these heavily populated areas (Greenlee and Langenheim 1990).

Deviation from the natural fire frequency may alter the relative proportions of shrubs in the chaparral canopy by favoring obligate seeding *Arctostaphylos* species over crown sprouters (Keeley and Zedler 1978) and taller, longer-lived *Arctostaphylos* over *Ceanothus, Adenostoma,* or *Salvia* (Davis 1972; Davis et al. 1988). The long absence of fire may eventually favor crown sprouting species such as *Quercus* and *Heteromeles* over obligate seeders (Keeley 1992b; Zammit and Zedler 1993). Fire frequency also affects the composition of the chaparral understory, both through the direct effects of heat, smoke, and ash, and indirect effects such as reduced competition and herbivory (Sweeney 1956, Christensen and Muller 1975a; Keeley and Keeley 1987; Tyler 1996).

Chaparral remnants in the coastal sandhills of north Monterey County between the communities of Pajaro and Prunedale are dominated by *Arctostaphylos pajaroensis* J. Adams and include several other uncommon species (Table 1). These stands continue to be fragmented and degraded by agricultural conversion and residential development, and their preservation is considered a high priority by Monterey County and by conservation organizations (Monterey County Planning Department 1981; Elkhorn Slough Foundation 1999). Unfortunately, little is known about the long-term effects of changing disturbance regimes on this unusual vegetation community.

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TABLE 1. UNCOMMON PLANTS OF PRUNEDALE HILLS MARITIME CHAPARRAL. [1] California Department of Fish and Game 2001; Skinner and Pavlik 1994.

Species	Rarity[1]
Arctostaphylos hookeri ssp. *hookeri*	CNPS List 1B (rare, threatened, or endangered)
Arctostaphylos pajaroensis	CNPS List 1B
Ceanothus cuneatus var. *rigidus*	CNPS List 4 (watch list)
Chorizanthe pungens var. *pungens*	Fed. threatened; CNPS List 1B
Ericameria fasciculata	CNPS List 1B
Piperia yadonii	Fed. endangered; CNPS List 1B

The objective of this study was to identify changes in community composition, canopy cover, and seedling abundance that occur in maritime chaparral stands during long periods of fire suppression and habitat fragmentation. The existence of field data from a 25-year old survey of maritime chaparral in the Monterey Bay region (Griffin 1978) provided a unique opportunity to compare historical vegetation data with current conditions. Most previous studies of chaparral dynamics in the absence of fire have relied on a chronosequence of sites (e.g., Zammit and Zedler 1988; Keeley 1992a, b) that may vary along abiotic or biotic gradients.
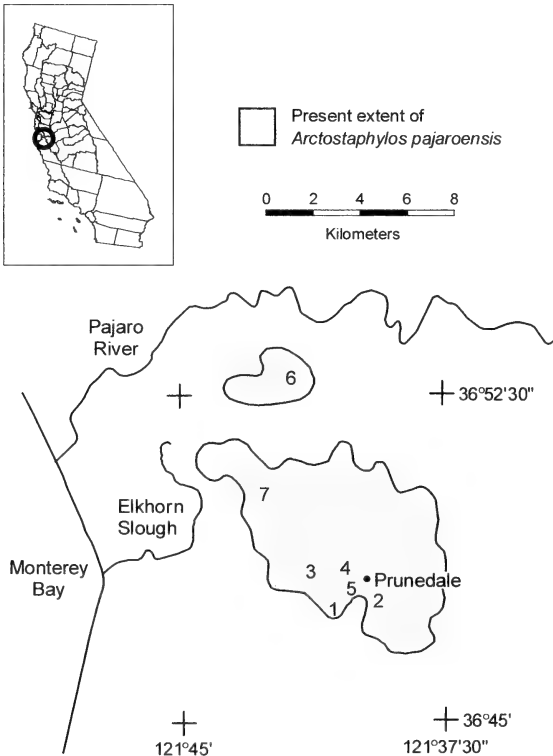
FIG. 1. Location of stands surveyed and present extent of *Arctostaphylos pajaroensis*. For descriptions of numbered stands see Table 2.

STUDY AREA

Griffin (1978) surveyed maritime chaparral stands in the Monterey Bay region between October 1975 and March 1977 using the Braun-Blanquet minimal-area relevé method (Mueller-Dombois and Ellenberg 1974). Between five and ten plots were sampled in the least disturbed portions of each of these stands. Seven stands were within the range of *Arctostaphylos pajaroensis* in the Prunedale sandhills.

In spring and summer 2000, we re-surveyed the seven Prunedale area stands (Fig. 1, Table 2). Griffin's field data and sketch maps for five of the stands, along with historic aerial photographs, allowed us to re-locate 50 plots to within a few meters of the original. Of these, 21 no longer contained maritime chaparral due to development. In the two stands where there was insufficient information to permit exact re-location, we selected 18 plots with slope, aspect, and substrate matching the original. Plots were identified on topographic maps to avoid selection bias and adjusted in the field only as necessary to avoid edge effects from roads or other human disturbance.

Davis (1972) estimated that approximately 50 years had elapsed since the last major fire in the Prunedale hills region by counting annual growth rings in mature *A. pajaroensis*. We verified that none of our study plots have burned during the past 70 years by examining historic vertical aerial photographs of each stand taken at intervals between 5 and 12 years beginning in May 1931.

Maritime chaparral stands in the Prunedale hills occur within a matrix of oak woodland and coastal sage scrub. The chaparral comprises two distinct plant associations. The 1932 Vegetation Type Map survey (US Forest Service 1932) distinguished a shorter "dwarfed chamise type" and a taller "chaparral type". Exposed plateaus, ridges, and sandstone outcrops support a patchy chaparral that rarely exceeds one meter in height and where *A. hookeri* G. Don ssp. *hookeri* and *Adenostoma fasciculatum* Hook & Arn. are dominant. On slopes and in depressions below the ridgelines, a tall, dense *A. pajaroensis* canopy predominates. Boundaries between these two chaparral types are typically quite abrupt. The majority of plots sampled for this study

TABLE 2.   PRUNEDALE HILLS MARITIME CHAPARRAL SAMPLING LOCATIONS.

Stand	Description	Number of plots	
		1975–6	2000
1	McGuffie Road	10	6 original plots; 4 plots lost to development
2	Vierra Canyon	10	3 original plots; 7 plots lost to development
3	Castroville Boulevard	7	10 approximate plot locations
4	Manzanita Circle	10	10 original plots
5	Prunedale	10	10 original plots
6	Lewis Road	10	10 plots lost to development
7	Hidden Valley	5	8 approximate plot locations

are composed of the *A. pajaroensis* dominated association.

Soils at the Prunedale hills are Arnold-Santa Ynez complex, a mixture of deep, excessively drained, slightly acid loamy sand derived from old marine dunes and soft, weathered sandstone outcrops (US Department of Agriculture 1978). Slopes vary from flat on plateaus and ridges up to 40 percent. Elevation ranges from 50 to 150 m. The distance of Monterey Bay is between 7 and 11 km. Mean precipitation is 50 cm, falling mainly during the winter months (Monterey County Water Resources Agency). Summers are dry, moderated by frequent fog.

METHODS

We employed Griffin's (1978) sampling techniques to facilitate comparison. Forty-seven 10 × 10 m square plots were delineated and all vascular plant species identified. Three height strata were distinguished: tree layer (rising above the shrub canopy), shrub layer (the chaparral canopy), and herb layer (the understory). At every plot, we recorded an estimate of the average canopy height and the percentage of vegetation cover for all three layers. We ranked every species in each layer according to the Braun-Blanquet cover-abundance scale: "r" = 1 individual, "+" = few individuals, "1" = 1–5% cover, "2" = 5–25% cover, "3" = 25–50% cover, "4" = 50–75% cover, "5" = 75–100% cover (Mueller-Dombois and Ellenberg 1974). A single species might occupy more than one layer. Adult *Quercus,* for example, contribute to the tree layer, saplings contribute to the shrub layer, and seedlings to the herb layer. In both surveys, all species of annual and perennial grass were combined into two categories. Additional species observed nearby but outside the plots were recorded separately; these species are included in Appendix 1, but not in quantitative analyses. Nomenclature is according to *The Jepson Manual* (Hickman 1993).

We calculated a "coefficient of community similarity" according to Jaccard (Mueller-Dombois and Ellenberg 1974) to compare species present in the tree and shrub layers among the plots of each survey and between the 1975–1976 and 2000 surveys at individual plots. We also calculated differences in mean percent cover for the combined tree and shrub layers and for individual tree and shrub species between the plots of the two surveys. Because a Braun-Blanquet scale value represents a range of percentages, we used the median of each class (e.g., 62.5% for rank "4", which represents 50–75% cover). The two lowest Braun-Blanquet scale values represent number of individuals rather than cover; we chose cover percentages of 0.1% for rank "r" and 0.5% for "+". We applied paired *t*-tests to arcsine-transformed percentages to determine the significance of each change in tree and shrub cover (Sokal and Rohlf 1995). As an index for comparing community similarity based on percent cover, we calculated "percent similarity" (Wolda 1981) between the plots of each survey and between the two surveys. We calculated changes in the herb layer using Braun-Blanquet scale ranks rather than estimates of percent cover because converting abundance to cover for the two lowest classes could be misleading where overall percentages are low.

For the 2000 data, we tested whether the number of species present at each stand was dependent on average canopy height or mean percent cover using linear regression. The 1975–1976 data did not include canopy height, so comparison between the two surveys was not possible. Nearly all plots tend to south facing, although their slopes vary considerably. We used linear regression to test whether changes in species composition or canopy cover were dependent on slope or aspect. Variations in soil type, relative elevation, and distance inland were minimal between plots, so the effects of these variables were not tested.

RESULTS

A total of 20 plant species were present in the tree and shrub layers of all plots in the 1975–1976 survey; 19 species were present in 2000. All species encountered both in and near the sample plots are listed in Appendix 1. Three shrub species that were uncommon in the earlier survey, *Ceanothus*
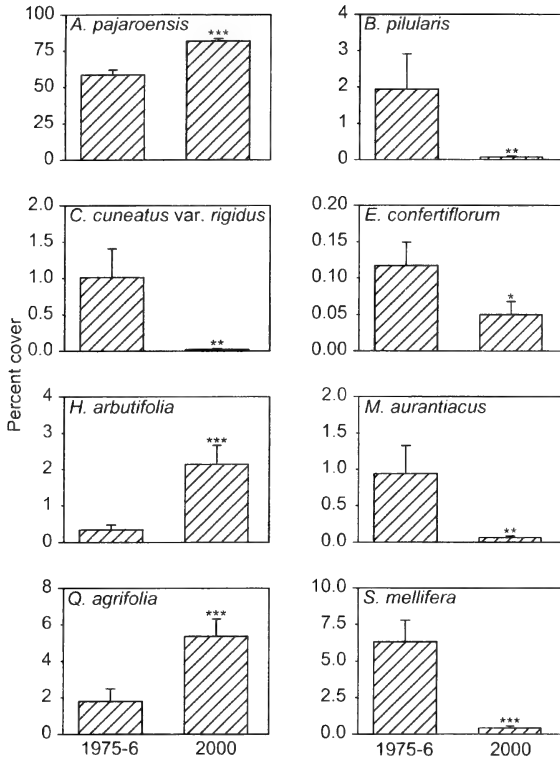
Fig. 2. Change in mean percent cover between 1975–6 and 2000 for selected species. * = P < 0.05; ** = P < 0.01; *** = P < 0.001 from paired *t*-test on arcsine-transformed percentages. Error bars indicate ±1 standard error. Note different y-axis scales.

cation was approximate, suggesting that these locations were somewhat mismatched.

Mean percent cover of the combined tree and shrub layers increased from 86 to 99% during the 25-year period (*t* = 6.5, P < 0.0001). This increase in canopy cover was chiefly due to a growing dominance by *Arctostaphylos pajaroensis* in nearly every plot. Mean cover of *A. pajaroensis* increased from 58 to 82% (t = 7.34, P < 0.0001, Fig. 2). Large increases in percent cover were also recorded for *Quercus agrifolia, Heteromeles arbutifolia, Rhamnus californica* Eschsch., and *Garrya elliptica* Lindley, but the total contribution of these oak woodland-associated sclerophylls remained small. Percent cover for all other shrubs decreased. Leading this decline was *Salvia mellifera* E. Greene, which dropped from 6.0 to <0.5% (t = 4.48, P < 0.0001). The percent similarity index confirmed a dramatic increase in homogeneity among the plots, from 0.61 in 1975–6 to 0.92 in 2000.

In the herb layer, overall species richness decreased from 27 species in 1975–6 to 18 in 2000, and the average number of species per plot decreased from 2.8 to 1.7 (t = 2.54, P = 0.015, Table 3). All five tree and shrub species that had seedlings present in the earlier survey also had seedlings present in 2000, and three of these, *Mimulus aurantiacus, Q. agrifolia,* and *Toxicodendron diversilobum* (Torrey & A. Gray) E. Greene, were more numerous and widespread (Table 4).

The Braun-Blanquet cover-abundance rankings for most subshrubs, herbs, and grasses decreased, as did the number of plots where they were found (χ^2 = 6.1, P = 0.047 for all species, Table 4). The fern *Pteridium aquilinum* (L.) Kuhn var. *pubescens* L. Underw. showed the largest decline, from up to 15 percent cover in each of 12 plots down to just a few individuals in four plots. More than half of the annual and perennial herbs counted in 1975–1976 were no longer present in 2000.

The number of species present in a plot was inversely related to canopy height (*F* = 8.87, R^2 = 0.16, P = 0.005) and to percent cover (*F* = 9.14, R^2 = 0.17, P = 0.004). Regression revealed no significant relationship between number of species or percent cover and slope or aspect.

Non-native species were not major constituents of intact maritime chaparral in the Prunedale hills. Introduced annual grasses such as *Bromus* spp.

dentatus Torrey & A. Gray, *C. thyrsiflorus* Eschsch., and *Ericameria ericoides* (Less.) Jepson, were absent from the 2000 survey. The shrub *Vaccinium ovatum* Pursh and the introduced tree *Pinus radiata* D. Don were not encountered in 1975–1976 and were rarely present in 2000. The average number of species per plot was nearly unchanged, increasing from 6.2 to 6.4. The Jaccard index, which compares the number of species in common, showed greater similarity for plots between the two surveys (0.81) than among the 1975–1976 plots (0.65) or among the 2000 plots (0.69). Jaccard indices were lowest at the two stands where re-lo-

TABLE 3. HERB LAYER: TOTAL NUMBER OF SPECIES AND MEAN NUMBERS OF SPECIES PER PLOT. * = P < 0.05; *** = P < 0.001 from paired *t*-test. ±1 standard error in parentheses. For species included in each category see Appendix 1.

Category	Total species			Species per plot	
	1975–6	2000	Common	1975–6	2000
Tree and shrub seedlings	5	5	5	0.27 (0.09)	0.73 (0.13)*
Perennial subshrubs, herbs, and grasses	18	11	8	2.37 (0.31)	0.94 (0.18)***
Annual herbs and grasses	4	2	1	0.15 (0.07)	0.04 (0.04)
All species	27	18	14	2.78 (0.39)	1.7 (0.24)*

TABLE 4. HERB LAYER: NUMBER OF PLOTS IN EACH BRAUN-BLANQUET COVER-ABUNDANCE CLASS. For additional species included in each category see Appendix 1.

Category and selected species	1975–6			2000		
	"r"	"+"	"1"–"2"	"r"	"+"	"1"–"2"
Tree and shrub seedlings	7	4	0	10	25	0
Baccharis pilularis	2	2	0	2	0	0
Mimulus aurantiacus	1	0	0	4	7	0
Quercus agrifolia	3	0	0	2	13	0
Rhamnus californica	1	0	0	1	0	0
Toxicodendron diversilobum	0	2	0	1	5	0
Perennial subshrubs, herbs, and grasses	23	66	8	15	30	0
Gnaphalium spp.	6	6	0	2	0	0
Helianthemum scoparium	0	5	0	0	0	0
Lotus scoparius	3	9	0	2	3	0
Marah fabaceus	0	0	0	3	6	0
Pteridium aquilinum	0	4	8	0	4	0
Annual herbs and grasses	0	6	0	0	2	0
All species	30	76	8	25	57	0

were occasionally present in plots in the earlier study, as they were in 2000. No exotic trees, shrubs, or herbs were counted in 1975–1976, although Griffin (1978) noted that *Carpobrotus edulis* (L.) N.E.Br., *Cortaderia jubata* (Lemoine) Stapf, and *Genista monspessulana* (L.) L. Johnson were invading nearby disturbed areas. In 2000, *C. jubata* was widespread near all of the sampling locations, although only one individual appeared within the study plots. Introduced *Pinus radiata* grew near three of the sites, and a single sapling was present in one plot. Large numbers of *Eucalyptus globulus* Labill. saplings were present in chaparral near three of the stands in 2000.

DISCUSSION

Maritime chaparral stands in the Prunedale hills have undergone significant changes in community composition, canopy cover, and seedling abundance between 1975–1976 and 2000, a period during which fire has been excluded. In the 1970's, the vegetation was patchy. Trees large enough to rise above the shrub layer were uncommon. *Arctostaphylos pajaroensis* competed with several other shrubs for dominance. A variety of grasses and forbs contributed to a sparse but widespread herb layer under the broken canopy. Today, the tree and shrub layers approach 100 percent cover forming a dense, closed canopy. *Arctostaphylos pajaroensis* is now the overwhelming dominant, although *Quercus agrifolia* cover has also increased significantly. The understory is generally bare except for occasional *Q. agrifolia* and *Mimulus aurantiacus* seedlings. Most herb layer species are restricted to the few remaining canopy gaps. All three of these trends, increased dominance by *A. pajaroensis,* loss of species diversity, and invasion by *Q. agrifolia,* may be attributed to the long absence of fire in the Prunedale hills.

Arctostaphylos pajaroensis dominance. The dramatic increase in *A. pajaroensis* cover, and similarly dramatic decreases for several other shrubs, likely result from the greater relative height of this long-lived species when freed from periodic destruction by wildfire. Davis (1972) noted that, with sufficient time and in the absence of fire, the stature of *A. pajaroensis* exceeds that of all other associated species except *Q. agrifolia.* This competitive advantage is largely due to the adaptation of "bark striping", where the amount of living tissue on stems in the lower, shaded portions of the shrub is minimized while providing structure to support the growth of new leaves and branches in full sunlight above (Davis 1973). We encountered a tangle of dead *Salvia, Adenostoma, Ceanothus,* and other shrubs in plots wherever the canopy exceeded two meters in height, suggesting the fate of these shorter species as they become overtopped and shaded by *A. pajaroensis.* McPherson and Muller (1967) described a similar competition for light in mature coastal chaparral in which shorter *Salvia* were progressively killed by taller shrubs. The dominant in this case was *Ceanothus cuneatus* (Hook.) Nutt., a species that also exhibits the bark striping strategy (Keeley 1975). Interestingly, in the Prunedale hills *C. cuneatus* var. *rigidus* (Nutt.) Hoover is one of the species that is overtopped and killed by taller *A. pajaroensis.*

Herb layer composition. Declining species richness and abundance in the understory are probably consequences of greater canopy height and density, and the resulting shade and litter accumulation, rather than differences in precipitation. Griffin (1978) suggested that the herb layer did not develop fully in 1975–1976, a drought year, yet he recorded a wider diversity of species growing under and among the trees and shrubs than we encountered in 2000, a normal rainfall year (Monterey County Water Resources Agency).

Many studies have commented on the absence of herbs and shrub seedlings under mature, undisturbed chaparral (e.g., Sampson 1944; Christensen and Muller 1975b; Hanes 1988). Competition for light, moisture, and nutrients and high levels of herbivory are common explanations (e.g., McPherson and Muller 1969; Schlesinger and Gill 1980; Swank and Oechel 1991; Tyler 1996; Keeley 2000). *Arctostaphylos* may also be a source of allelopathic substances, inhibiting the establishment of seedlings under the chaparral canopy (Muller et al. 1968, Chou and Muller 1972). The only herbaceous species that showed a significant increase in the shade under dense *A. pajaroensis* was *Marah fabaceus* (Naudin) E. Greene, a vine that resprouts annually from a large underground tuber and can quickly reach sunlight in the shrub canopy (Schlising 1969).

Two annual herbs, *Chorizanthe pungens* Benth. var. *pungens* and *Navarretia hamata* E. Greene, and three perennial shrubs or subshrubs, *Eriophyllum confertiflorum* (DC.) A. Gray, *Helianthemum scoparium* Nutt., and *Lotus scoparius* (Nutt.) Ottley, were restricted to openings in the canopy in 2000. Canopy gaps are important for seed germination and seedling establishment and for maintaining the seed banks of many chaparral species (Davis et al. 1989; Zammit and Zedler 1994; Odion and Davis 2000). As tree and shrub layer cover has increased, gaps have grown increasingly rare.

Quercus agrifolia *invasion.* An increase in *Q. agrifolia* canopy cover and seedling abundance in Prunedale hills maritime chaparral stands is consistent with Keeley's (1992a, b) conclusion that species like *Q. agrifolia* that are capable of regeneration from root crowns will only produce seedlings after a long fire-free period, and only under a dense canopy in a heavy accumulation of leaf litter. Callaway and D'Antonio (1991) found that shrubs frequently serve as "nurse plants", providing microhabitat conditions that facilitate the establishment of *Q. agrifolia* seedlings that will eventually overtop and kill their hosts. We frequently encountered mature *Arctostaphylos* skeletons in the shaded understory of oak woodland immediately adjacent to chaparral stands, an observation also reported by Davis (1972).

Boundaries between chaparral, coastal sage scrub, and oak woodland communities are dynamic and highly dependent on fire frequency (Gray 1983; Callaway and Davis 1993). Live oak woodland is widely characterized as the successional climax for maritime chaparral stands in the absence of fire (e.g., Wells 1962; Davis 1972; McBride and Stone 1976; Griffin 1978). Several studies suggest that a gradual transition to oak woodland is underway at various locations on the central coast as *Q. agrifolia* invades long unburned areas (Davis et al. 1988; Callaway and Davis 1993; Mensing 1998; White 1999). Various studies have also proposed that the segregation of maritime chaparral and oak woodland communities is at least partially due to edaphic differences (e.g., Wells 1962; Cole 1980; Davis et al. 1988). Davis (1972) and Griffin (1978) both conclude that *Q. agrifolia* is successional to the more mesic *A. pajaroensis* association in the absence of fire, while conversion from chaparral to oak woodland will progress more slowly, and perhaps even be arrested, in the more xeric *A. hookeri* association. Even on the harshest sandstone ridges, *Q. agrifolia* is occasionally present, but only as seedlings and shrub-sized individuals.

Long-term vegetation changes in the absence of *fire.* As was the case in 1975–1976, no recruitment of obligate seeding *Arctostaphylos* or *Ceanothus* species was observed in any of our study plots in 2000. The only seedlings of these taxa that we encountered anywhere during this survey were a few dozen young *A. pajaroensis* and *C. dentatus* that had established near one of the plots in a small area that had burned two years previously. These results are not surprising as seeds of several species in these two genera are reported to require heating or exposure to smoke or charate to stimulate germination (Keeley 1987; Keeley and Keeley 1987; Keeley and Fotheringham 1998).

The effect of long fire-free periods on chaparral is a topic of considerable discussion. Keeley (1992a) has persuasively argued that pejorative terms such as decadent and senescent that are often applied to long-unburned chaparral stands (e.g., Sampson 1944; Hanes 1988) are inappropriate for describing a gradual successional shift from obligate seeding *Arctostaphylos* and *Ceanothus* species to crown sprouting *Quercus* and *Heteromeles.*

Keeley (1992a) also notes the importance of variable fire regimes to maintain equilibrium in species composition. The long absence of fire may lead to local extinction of certain species if soil seed banks become exhausted. The length of time that seeds remain viable is unknown for most maritime chaparral species (Tyler and Odion 1996). Further study of seed bank longevity is needed to understand the risk to species of concern such as *C. cuneatus* var. *rigidus, Chorizanthe pungens* var. *pungens, Ericameria fasciculata* (Eastw.) J.F. Macbr., and *Piperia yadonii* R. Morgan & J. Ackerman.

Because the majority of Prunedale hills maritime chaparral has not burned for at least 70 years, we feel that concern for the future of *A. pajaroensis, C. cuneatus* var. *rigidus,* and the other plants that characterize this unusual vegetation community is warranted. Neither they nor their seeds can survive forever. If wildfire continues to be excluded, the composition of these stands will undoubtedly be very different in the future.

Management implications. Griffin (1978) concluded with this warning: "Pressures for development are so great around Monterey Bay that maritime chaparral stands need legal protection to survive. No adequate sample of chaparral near Prunedale has formal protection now." Since this writing,

several important Prunedale hills stands have received protection as conservation lands. At the same time, additional chaparral acreage is lost every year and development pressures continue to grow. Of the seven original 1975–1976 sampling areas, three are highly modified with only fragments of undisturbed chaparral remaining, two had remained relatively intact but currently have subdivision plans underway, and two are within the boundaries of Manzanita County Park where sports facility expansion is proposed.

Areas dominated by the low *A. hookeri* chaparral association are generally unsuited for agriculture because of their shallow soils and remain as fragments along ridgelines throughout the Prunedale hills. Monterey County land use policies discourage development on ridges and encourage the dedication of scenic and conservation easements on unbuildable portions of subdivisions that contain these maritime chaparral fragments (Monterey County Planning Department 1981). Stands of the taller *A. pajaroensis* association, because they occur on the gentler south-facing slopes and deeper soils favored for cultivation, have been lost to agricultural conversion over a period of many decades. In recent years, a shortage of land suitable for residential development in north Monterey County has accelerated the destruction of this chaparral type. Alternative management strategies are needed for these two different chaparral types.

Loss of species diversity caused by shading is associated with canopy height, thus with the *A. pajaroensis* dominated chaparral type. Invasion by *Q. agrifolia* is also rapid in these more mesic sites. For these areas, the introduction of prescribed burning, or perhaps mechanical disturbance with smoke or charate treatment, may be necessary to open the canopy, facilitate seedling establishment, and slow the advance of oaks. Enhancement of the seed bank with stockpiled chaparral soil, in conjunction with burning, could be necessary in degraded areas (Odion 1995). Unfortunately, non-native species often follow disturbance in chaparral (Zedler and Scheid 1988; D'Antonio et al. 1993; Tyler and Odion 1996; Holl et al. 2000), so a control program would likely be required. In the low *A. hookeri* chaparral type, where gaps are frequent and *Quercus* grow slowly, prevention of any kind of disturbance might be the more appropriate management strategy.

Land protection is the essential first step toward conserving increasingly rare maritime chaparral communities. Conservation efforts should focus on stands that include both chaparral associations. Active land stewardship will also be necessary in order to conserve the full complement of native plant species. Management strategies should attempt to maximize diversity by maintaining a variety of successional stages and canopy heights including bare rock and soil, patchy mixed chaparral, closed *Arctostaphylos* canopy, and mixed chaparral/oak

woodland. The effects of a modified disturbance cycle in the Prunedale hills will need to be understood in order to ensure the survival of this unusual vegetation and to minimize the loss of endemic species.

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APPENDIX 1.

SPECIES ENCOUNTERED AT PRUNEDALE HILLS MARITIME CHAPARRAL SAMPLING LOCATIONS. [1] = present in plots 1975–6, [2] = present in plots 2000, [3] = present in plots both surveys. Species without numbers in brackets were observed near but never in plots.

Trees:

Eucalyptus globulus (non-native)
Pinus radiata (introduced) [2]
Quercus agrifolia [3]
Quercus wislizenii

Shrubs:

Adenostoma fasciculatum [3]
Arctostaphylos hookeri ssp. hookeri [3]
Arctostaphylos pajaroensis [3]
Arctostaphylos tomentosa ssp. crustacea [3]
Artemisia californica
Baccharis pilularis ssp. consanguinea [3]
Ceanothus cuneatus var. rigidus [3]
Ceanothus dentatus [1]
Ceanothus thyrsiflorus [1]
Chrysolepis chrysophylla
Dendromecon rigida [3]
Ericameria ericoides [1]
Ericameria fasciculata [3]
Eriophyllum confertiflorum [3]
Garrya elliptica [3]
Genista monspessulana (non-native)
Heteromeles arbutifolia [3]
Lepechinia calycina
Mimulus aurantiacus [3]
Pickeringia montana [3]
Rhamnus californica [3]
Salvia mellifera [3]
Solanum umbelliferum
Symphoricarpos mollis
Toxicodendron diversilobum [3]
Vaccinium ovatum [2]

Perennial subshrubs, herbs, and grasses:

Achillea millefolium [1]
Calochortus albus
Cardionema ramosissimum

Carex spp. [1]
Carpobrotus edulis (non-native)
Castilleja foliolosa
Chlorogalum pomeridianum
Cortaderia jubata (non-native) [2]
Dichelostemma capitatum
Dudleya lanceolata [3]
Eriogonum nudum
Galium californicum [1]
Gnaphalium spp. [3]
Helianthemum scoparium [1]
Horkelia cuneata [1]
Iris douglasiana
Lessingia filaginifolia
Lomatium sp. [1]
Lotus scoparius [3]
Lupinus spp.
Marah fabaceus [2]
Oxalis albicans ssp. pilosa
Pedicularis densiflora [3]
Pellaea mucronata [1]
Pentagramma triangularis [3]
perennial grass [3]
Piperia yadonii
Polygala californica [3]
Pteridium aquilinum var. pubescens [3]
Rosa gymnocarpa [2]
Rubus ursinus [1]
Rupertia physodes
Scrophularia californica [1]
Scutellaria tuberosa
Sisyrinchium bellum
Solidago sp. [1]
Zigadenus fremontii var. fremontii

Annual herbs and grasses:

annual grass [1]
Camissonia spp.
Chorizanthe pungens var. pungens [2]
Cryptantha sp.
Hemizonia sp. [1]
Linaria canadensis
Lupinus spp.
Madia sp. [1]
Navarretia hamata [3]

THE EFFECTS OF LITTER AND TEMPERATURE ON THE GERMINATION OF NATIVE AND EXOTIC GRASSES IN A COASTAL CALIFORNIA GRASSLAND

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Abstract

Through their effects on seed germination, accumulation of plant litter and temperature may play a role in the invasion of coastal California grasslands by exotic annual and perennial grasses. Germination of native and exotic grasses was examined as a function of both litter cover and temperature. When species were grouped by life form (native perennial grass vs. exotic perennial grass), exotic species germinated at consistently higher rates than native species. Individual species, however, varied in their response to litter addition. While one exotic perennial species, *Festuca arundinacea*, maintained germination rates significantly higher than native species' across three levels of litter cover, the other exotic perennial species, *Holcus lanatus*, showed no advantage over native species in the presence of a heavy litter layer. Exotic annual grasses had significantly higher germination rates than native perennial or exotic perennial grasses in laboratory growth chambers. Decreasing the average fall temperature in laboratory growth chambers by 5°C significantly reduced the germination percentages of *Bromus diandrus* and *F. arundinacea* relative to other species. The remaining two exotic annual grasses, *Avena barbata* and *Vulpia myuros*, were consistently the first seeds to germinate. Grouping species according to life form masked germination responses of individual species that otherwise provide insight into the potential role of germination conditions in community composition of coastal grasslands in California.

Introduction

The invasion of exotic grasses has substantially altered the species composition of California grassland ecosystems. Currently, seven million hectares in California are vegetated by European annual grasses, yet it is thought that, prior to European settlement, much of this area was dominated by perennial bunchgrasses (Burcham 1970; Heady et al. 1988; Baker 1989). Native perennial-dominated grasslands that have resisted invasion by European annual species are currently rare in California, though several native grasslands have persisted in northern coastal California (Ornduff 1974; Hektner and Foin 1977; Dremann 1988). Recently, invasion by exotic perennial grass species such as *Holcus lanatus* L. and *Festuca arundinacea* (Schreber) has further threatened these remnant native grasslands (Elliot and Wehausen 1974). Exotic perennial species may be of equal or greater threat than exotic annual species since their larger investment in vegetative structures enables the maintenance of dominance once they become established (Jackson and Roy 1986).

The importance of early life stages in exotic invasions has been demonstrated in a variety of ecological systems (Parker 2000; Ruiz et al. 2000). Germination and seedling establishment are likely to be especially crucial phases in the invasion of grasslands by long-lived perennial species (Fowler 1986), though little is known about the factors that influence the seed germination of exotic perennial species in California. Climatic conditions, especially temperature and rainfall at the time of seed germination, have been shown to play a role in year-to-year variation in species composition of exotic annual grass- and exotic forb-dominated habitats in California (Heady 1958; Pitt and Heady 1978; Jackson and Roy 1986; Young and Evans 1989). Soil disturbances, such as those created by gopher activities, provide open spaces that facilitate both native and exotic seedling establishment in California (Platt 1975; Hobbs and Mooney 1985; Peart 1989; Kotanen 1996). The accumulation of plant litter, which has been shown to have both positive and negative effects on seed germination, also affects species composition of grasslands (Young et al. 1971; Hamrick and Lee 1987; Facelli and Pickett 1991a, b; Foster and Gross 1998). These factors, climatic conditions, availability of openings at the soil surface, and litter quantities, are likely to vary across the landscape and from year to year, and could influence the ability of exotic perennial species to invade grassland habitats.

To examine the response of exotic perennial grass species to variation in micro-environmental and climatic conditions, we compared the germination rates of native and exotic grass species under three levels of litter addition and at three different temperatures. Our experimental design allowed us to compare the germination responses of each species across a range of environmental conditions, and to examine conditions influencing germination and establishment of exotic species. We used seeds

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from four native perennial grass species, three common exotic annual species and two of the most abundant exotic perennial grasses in this part of California, *H. lanatus* and *F. arundinacea*.

METHODS

Study site. The field portion of this study was conducted at Tom's Point, a private nature preserve adjacent to Tomales Bay in northern Marin County (38°13′N, 122°57′W). The vegetation of this coastal prairie community consists of European annual grasses and forbs with interspersed stands of native perennial bunchgrasses. The site is located on sandy loam soils and has been free of livestock grazing for at least 30 years. The climate is Mediterranean with an average annual temperature of 16°C, dropping only slightly in January and February. Rainfall totals are approximately 800 mm/ year, falling predominantly between October and April. Coastal fog present in the summer months moderates the summer drought. *Deschampsia caespitosa* ssp. *holciformis* (C. Presl and W.E. Lawr), *Festuca rubra* L., *Calamagrostis nutkaensis* (C. Presl and Steudel), and *Nassella pulchra* (A. Hitch. and Barkworth) are the most common native species at the site. The most common exotic perennial species are *F. arundinacea* and *H. lanatus,* and the most common exotic annual species are *Avena barbata* L., *Bromus diandrus* (Roth), and *Vulpia myuros* var. *myuros* (c. Gmelin).

All seeds for the experiment were collected in either July 1998 or July 1999. Seeds collected in 1998 were stored at room temperature for one year. Seeds collected in 1999 were stored at room temperature for one month. Lab trials prior to experimentation confirmed the viability of both sets of seeds. We used *H. lanatus* leaf and culm litter because current invasion of this species into both exotic annual and native perennial-dominated grasslands is resulting in large quantities of previously non-existent litter that appears to be relatively persistent in coastal grasslands. Litter was collected in September 1999.

Litter experiment. Seeds were added to three 1 m × 1.5 m experimental plots in October 1999 in an area of the grassland that had been cleared of background vegetation (predominantly *Conium maculatum* L.) in 1998 and again in 1999 just before planting. There was no gradient in soil moisture content (10 cm depth), inorganic nitrogen concentrations, or annual grass germination rates in the area where our plots were established (Corbin and D'Antonio, unpublished data). Germination rates of the four native and two exotic perennial species were compared across three litter treatment plots: bare soil, 1 cm of *H. lanatus* litter (200 g spread evenly over the plot), and 3 cm of *H. lanatus* litter (450 g spread evenly over the plot). Within each plot, 30 seeds of each of the six perennial species were planted in 10 cm × 10 cm subplots. Each

treatment plot contained six replicate subplots for each species, plus six unplanted subplots to control for germination from the seed bank or residual seed rain. The number of grass seeds emerging from the control plots was very low in all treatments (mean ± SD: 1.0 ± 1.0 seeds), and we concluded that there was no substantial seed bank for any of the species. Six soil cores (2 cm diameter × 1 cm deep) were collected in each plot to measure gravimetric soil moisture at the soil surface. Light levels at the soil surface of each plot were measured at noon on a clear November day with a LiCor light meter. In order to minimize seed predation and litter loss, a 1 cm mesh covering was placed over each treatment plot at a height of 25 cm. Emerged seedlings were counted 4 weeks, 6 weeks, and 10 weeks after planting. The maximum number of seedlings emerging in each subplot was used for analysis.

Temperature experiment. To test the effects of temperature on seed germination, we used growth chambers to simulate cold, average, and warm germination conditions in the field. Two exotic perennials, three native perennials, and three exotic annuals that are common at the study site were tested. Although the native perennial *D. caespitosa* ssp. *holciformis* was used in the litter experiment, it was not included due to space constraints. Cold and warm years were approximated at 5°C below and above the average fall temperature recorded at Bodega Marine Reserve (located 12 km north of Tom's Point) in October and November. Diurnally fluctuating temperature regimes were set at 9/3°C, 15/8°C, and 20/12°C for day/night temperatures in the cold, average, and warm manipulations, respectively. Temperature was monitored frequently using a mercury thermometer to ensure that the chamber reading was consistent with the air temperature. Chamber lights were programmed on a 24 hour cycle to match autumn daylight hours observed in the field. The relative humidity and light levels of the chambers were held constant across temperature treatments and monitored every two days. 20 seeds of each species were placed in 6 cm petri dishes upon three layers of filter paper and 10 g of white quartz sand. A thin layer of *H. lanatus* litter (approximately 0.5 cm) was added to all dishes to reduce desiccation. Ten replicate dishes of each species were randomly placed in each chamber. Dishes were watered every other day to keep the sand thoroughly dampened. The exact quantity of water added varied among chambers because evaporation rates differed slightly across temperature treatments. Germinating seeds were counted every three days for six weeks. Seeds were considered germinated when either the radicle or shoot became visible.

Statistics. Species' germination rates in each litter and temperature treatment were arcsin transformed and compared using two one-way ANOVA's, in which species and life form (exotic peren-
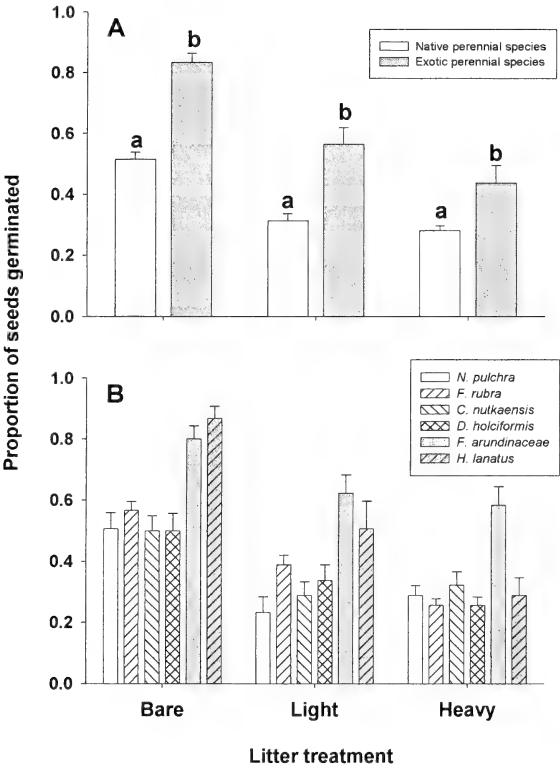
FIG. 1. Mean (±SE) proportion of seeds germinated in the three litter plots (no litter, 1 cm litter, and 3 cm litter) of A) life form groups and B) individual species. Letters denote significant differences between life form groups for each litter treatment according to Tukey's HSD (P < 0.05).

nial, exotic annual, or native perennial) were the main effects (JMP, SAS Institute). Pairwise comparisons between species and between life form groups were performed using Tukey's HSD. We did not compare species responses across litter or temperature treatments (i.e., species × temperature interactions in two-way ANOVA), since neither the litter treatment plots nor the temperature growth

chambers were replicated at the level of litter quantity or growth chamber temperature.

RESULTS

Effects of litter on germination rates

Exotic perennial species exhibited superior germination percentages compared to native perennial species in all three litter treatments (Fig. 1A). *F. arundinacea* germination rates were significantly greater than the rates of all four native species, with the exception of *F. rubra* in the light litter treatments (Fig. 1B; Table 1). The germination of *H. lanatus* was significantly higher than the germination of native species in the bare treatments only; otherwise *H. lanatus* germination was similar to that of the native species (Table 1).

Gravimetric soil moisture was significantly different between the three treatments ($F_{2,17} = 7.64$, P < 0.005), as were light levels ($F_{2,17}$, P < 0.0001). Plots with litter had higher soil moisture and lower light levels than the bare plots.

Effects of temperature on germination rates

When the species' germination percentages were pooled by life form group, exotic annual grasses had the highest and exotic perennial species had the lowest germination rates in all three temperature treatments (Fig. 2A). Native perennial species did not differ significantly from exotic perennial species. There was little difference between the relative germination percentages of each species in the average and +5°C growth chambers: two exotic annual species, *V. myuros* and *B. diandrus,* and one native perennial species, *F. rubra* had the greatest germination rates, while *H. lanatus* had the lowest rates in each temperature (Fig. 2B; Table 1). Temperatures 5°C below the average substantially reduced the germination percentages of *B. diandrus,* an exotic annual grass, and *F. arundinacea* relative to other species' germination percentages (Fig. 2).

There were species-specific patterns of germination over time. In the warm and average temper-

TABLE 1. PAIRWISE COMPARISONS BETWEEN SPECIES GERMINATION PERCENTAGES IN EACH LITTER AND TEMPERATURE TREATMENT. Letters denote significant differences between species within a treatment according to Tukey's HSD (P < 0.05). See Figure 2 for directions of the significant differences, and for pairwise comparisons between life form groups.

Species	Litter treatment			Temperature treatment		
	Bare	Light	Heavy	Warm	Normal	Cold
N. pulchra	a	a	a	ab	ac	ac
F. rubra	a	bc	a	b	ab	ab
C. nutkaensis	a	ab	a	ab	ac	ac
D. holciformis	a	ab	a	N/A	N/A	N/A
F. arundinacea	b	c	b	ab	ac	c
H. lanatus	b	bc	a	a	c	ac
V. myuros	N/A	N/A	N/A	c	d	d
A. barbata	N/A	N/A	N/A	ab	ac	b
B. diandrus	N/A	N/A	N/A	b	b	c
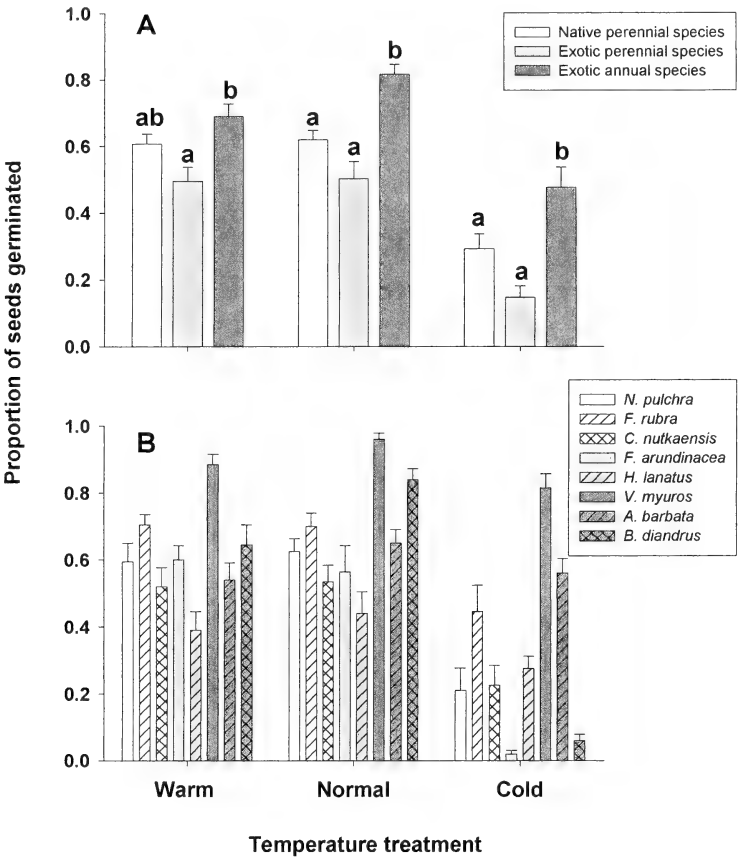
FIG. 2. Mean (± SE) proportion of seeds germinated in the three temperature treatments (warm, average, and cold) of A) life form groups and B) individual species. Letters denote significant differences between life form groups for each litter treatment according to Tukey's HSD (P < 0.05).

ature chambers, the three exotic annual species consistently were the fastest to germinate (Fig. 3). In the cold temperature chamber, two of the three (*Vulpia myuros* and *Avena barbata*) were still the first to germinate, while the third, *Bromus diandrus*, had extremely low germination. In the average temperature chamber the two exotic perennials (*F. arundinacea* and *H. lanatus*) germinated more rapidly than the native perennials (Fig. 3). Of particular note is that while the native perennial *F. rubra* exhibited a final germination rate 60% higher than the exotic perennial *H. lanatus, H. lanatus* seedlings emerged more quickly than did *F. rubra* seedlings (Figure 3).

DISCUSSION

Plant litter can affect germination and seedling establishment differently depending on physical and environmental conditions of the ecosystem (Facelli and Pickett 1991b). While litter has been shown to aid germination in dry grasslands and deserts by retaining surface soil moisture (Young et al. 1971; Fowler 1986), the majority of grassland litter manipulations demonstrate that litter has a negative effect on germination and seedling establishment of grasses in relatively mesic systems (Goldberg and Werner 1983; Tilman 1987; Gulmon 1992; Xiong and Nilsson 1999). The litter volumes used in this study are comparable to those of other grassland litter studies and match litter levels observed in the field (Fowler 1986; Carson and Peterson 1990; Xiong and Nilsson 1999). Our litter treatments were found to significantly increase soil moisture and decrease light levels to the soil surface. It is also likely that soil surface temperatures and barriers to seed emergence varied with litter treatments, though these effects were not measured.

Exotic perennial grasses germinated at higher rates than native perennial grasses in all three litter treatments. However, grouping species by life form masked individual species responses that may be important in understanding the dynamics of invasion by exotic grass species. Germination of *F. arundinacea* (one of the two exotic perennial species) was significantly higher than germination of the four native species in all three litter treatments. The other exotic perennial species, *H. lanatus,* germinated at a significantly higher rate than the four

FIG. 3. Mean proportion of each seeds germinated of individual species at three day intervals (0 to 51 days) for each temperature treatment.

minate equally well beneath litter accumulation as on bare soil, the species' intolerance of cooler temperatures at the time of germination suggests that weather patterns may have an effect on the establishment of this species in coastal grasslands of California. These findings have implications for restoration efforts because they suggest cooler years may provide a window of opportunity for establishing some native perennial species such as *F. rubra*.

Although interspecific competitive effects on seedling establishment were not tested in this study, differences in the timing of individual species' germination have been shown to be important in seedling establishment, since the first seedlings to emerge have greater access to space and resources leading to a higher survival probability (Ross and Harper 1972; Dyer et al. 2000). The early emergence of exotic annual species such as we observed in all three temperature chambers suggests that in a competitive field environment they may have an advantage over native perennial species such as *F. rubra, C. nutkaensis,* and *N. pulchra* because of shading of late germinating native species (Bartolome and Gemmill 1981; Dyer and Rice 1999).

Differences between native and exotic species' seed production, seed dispersal, response to microsite availability, and competitive abilities may be equally, if not more, important than germination requirements for understanding the dynamics of exotic perennial grassland invasion. However, our results suggest that given adequate seed supply and microsite availability, the amount of litter cover and temperature differentially affect the germination of individual native and exotic grasses. While the germination percentage of exotic species, seeds was consistently higher than that of native species, we predict that individual species' capacity to germinate, and, therefore, to become established, will vary from year to year and from habitat to habitat according to differences in litter cover and climatic conditions.

native species in the bare and light litter treatments, but was not significantly different from the natives in the heavier litter layer. The ability of *H. lanatus* to invade grasslands may, therefore, vary with litter accumulation from year to year or from habitat to habitat. Consistently high germination rates of *F. arundinacea* suggest that this species is capable of germinating under a wider range of conditions. It is currently widely distributed in the U.S. and is considered a threat to native plant assemblages in California (CALEPPC, 1999).

As seen in the analysis of the litter treatments, mean germination rates of species grouped by life form hid individual species' responses to variation in temperature. Exotic annual grasses had the highest germination rates in all temperature treatments, followed by native perennials and exotic perennials. However, a 5°C decrease in the average temperature at time of germination reduced germination rates of *F. arundinacea* and *B. diandrus* relative to the other species. Despite the low germination of *B. diandrus* in the cold temperature treatment, the ability of the other two annual grass species to tolerate a range of temperatures at the time of germination and annuals' rapid germination after wet-up may explain the expansive distribution of European annual grasses throughout California (Heady 1958; Pitt and Heady 1978; Young and Evans 1989). Although *F. arundinacea* can ger-

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COMPOSITION, INVASIBILITY, AND DIVERSITY IN COASTAL CALIFORNIA GRASSLANDS

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ABSTRACT

We present a detailed floristic study of coastal terrace prairies in central California that are poorly described in California's ecological literature. Definitive native grasses include *Danthonia californica* Bolander, *Nassella pulchra* (A. Hitchc.) Barkworth, and *Festuca rubra* L. Definitive native forbs include *Baccharis pilularis* DC., *Viola, Sidalcea, Cammisonia,* and *Acaena.* Species richness in the coastal prairies (1 m²) averaged 22.6, nearly twice that of relatively diverse serpentine California grasslands, and other North American grasslands. We sampled 33 coastal prairies and found 340 plant species including 258 forbs. Nearby plant communities (Monterey Pine, Coastal Scrub) had much lower species diversity at all spatial scales studied. Three distinct coastal grasslands, each associated with a land form, can be defined by distinct species composition; coastal terraces, uplifted "bald hills," and inland ridges. We compared 29 coastal terrace prairies (those without tree or shrubs) to 80 inland *Nassella* prairies with regard to 27 floristic variables (cover, number of natives/exotics, perennials/annuals, grasses/forbs) along a gradient from interior-coastal valley and from north to south along the coast. Coastal terrace prairies were invaded by exotics, but far less so than inland *Nassella* prairies. Species diversity (0.1 ha) and total cover were positively correlated. Relative cover of exotic species was negatively correlated with total cover, based on all sites. Number of exotic species was positively correlated with species richness in inland *Nassella* prairies but not in coastal terrace prairies. Canonical correspondence analysis indicated that coastal terrace prairies with higher cover of non-native species had reduced total cover and/or reduced diversity of native perennial species of grasses and forbs. Native perennial grasslands, including coastal terrace prairies, are rare and have been eliminated by development along the narrow corridor of land between the sea and the inland ridges of central, coastal California. If protection of biodiversity is a management goal in land use plans, coastal grasslands should be protected as biodiversity "hotspots".

INTRODUCTION

Native perennial grasslands in California are among the most endangered ecosystems in the United States (Peters and Noss 1995). An area of approximately 7,000,000 ha (about 25% of the area of California) formerly in native grassland or foothill savanna, is now dominated by exotic grass species primarily of Mediterranean origin (Huenneke 1989). Typical annual grassland species include *Bromus diandrus* Roth, *B. mollis, B. rubens* L., *Avena barbata* Link, *A. fatua* L., *Erodium cicutarium* (L.) L'Hér., *E. botrys* (Cav.) Bertol, and *Vulpia myuros* (L.) C. Gmelin (Heady et al. 1988). Conversion to exotic annual vegetation was so fast, extensive, and complete that the original extent and species composition of most native perennial grasslands is unknown (Burcham 1957; Barry 1972; Keeley 1989; Heady et al. 1992; Holland and Keil

1995). Cover of exotics is often over 80% in this annual grassland vegetation type (Biswell 1956). Yet, small, isolated stands of native perennial grasslands still occur and these stands have been used to define "valley grassland" (White 1966b, 1967; Robinson 1971), presumably once dominated by *Nassella* (Heady et al. 1988). Extensive fragmentation of relict grasslands continues (Barry 1972) and even within protected natural areas (Hastings, San Bruno Mountain, Jepson Prairie, Santa Rosa Plateau), relatively "pure" stands of native grasses occur in smaller, interior patches. Few studies have been published to describe the original grassland composition or that of presumed remnants. The widely held view that interior annual grasslands of California were originally dominated by perennial grasses (primarily *Nassella*) is based on limited evidence (Hamilton 1998). The view that succession proceeds in these interior grasslands to dominance

Monterey Bay

California

Morro Bay

| 0 | 95 | 190 | | 380 |

Km
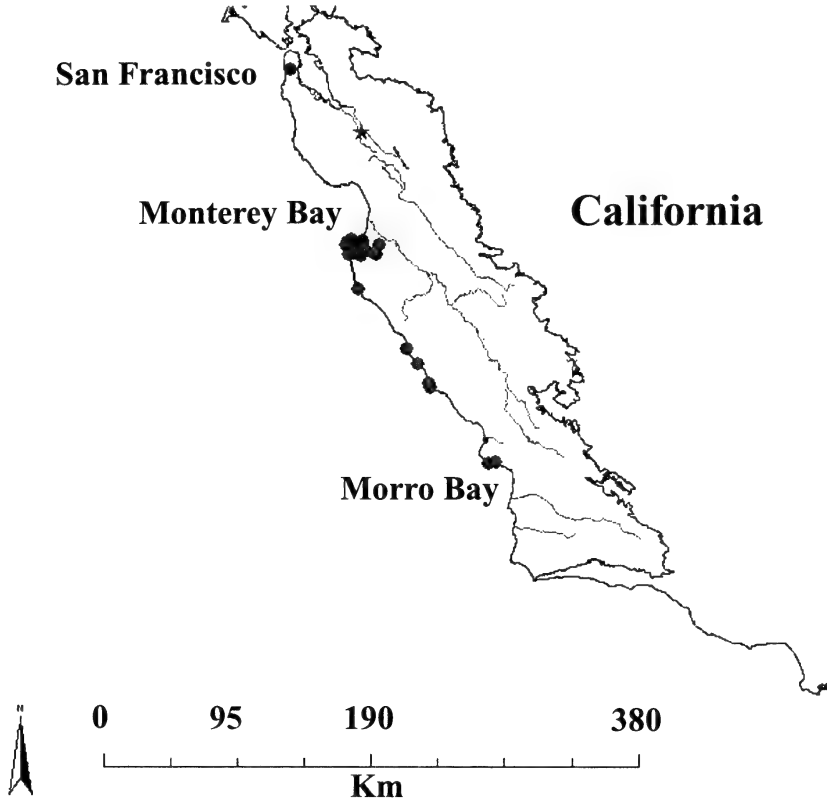
FIG. 1. Map of study sites on coastal California.

by *Nassella* (Heady et al. 1988) is not supported by long-term studies (Stromberg and Griffin 1996) or a critical review of evidence (Hamilton 1998). Large areas of the interior "valley grassland" (Heady et al. 1988) may have been dominated by native, annual forbs (Schiffman 1994; Schiffman 2000). Identification of these rare, scattered patches of high biodiversity continues to be a critical activity for conservation (Myers et al. 2000). GAP analysis and remote sensing serve as useful tools, but to identify the most important habitats at a finer geographic scale, we need intensive field surveys using classical methods, as presented here.

The purpose of this study is to demonstrate that California's coastal grasslands are previously unrecognized biodiversity hotspots. We will do this by presenting patterns of diversity, describing major gradients in diversity within habitats and compare the coastal grasslands with other nearby habitats and other United States grasslands.

California's coastal grasslands are poorly described in the literature. "Coastal terrace prairie" has had widely varying interpretations. (Kuchler 1964) described "coastal grasslands" in a general way. Others have defined "north coast prairies" by listing dominant species that extend from the Mendocino coast south to Point Lobos (Heady et al. 1988). They described north coast prairies as being dominated by *Festuca idahoensis* Elmer, *F. rubra*

and *Danthonia californica;* they used the term "coastal terrace prairie" to describe this community. "Northern coastal grassland community" with the same dominant grasses, as well as *Calamagrostis nutkaensis* (C. Presl) Steudel and *Deschampsia cespitosa* (L.) Beauv., has been described as extending from San Francisco northward to the Klamath Mountains and in patches south to San Luis Obispo (Holland and Keil 1995). Finally, a "tufted hairgrass community" has been defined where *Danthonia* is dominant—this series is part of the "coastal prairie, which extends inland from terraces to bald hills" (Sawyer and Keeler-Wolf 1995). Such "bald hills" are a common feature along the coast and arise abruptly inland from the coastal terraces. Coastal prairies occur on poorly drained soils, often clays derived from serpentine outcrops, and often occur on a series of former coastal terraces that through geological action have been moved inland and uplifted. As one moves inland, "ecological staircases" grade into drier, higher interior ridges (Westman 1975; Cylinder 1995). Most of these interior ridges are forested, but many sustain open grasslands. Further inland, conifer forests are replaced by oaks and typical "annual grassland" oak savanna (Barbour and Major 1995, Holland and Keil 1995). Monterey pine forests are often adjacent to coastal terrace prairies in the central coast of California. Shrubs (e.g., *Baccharis*)
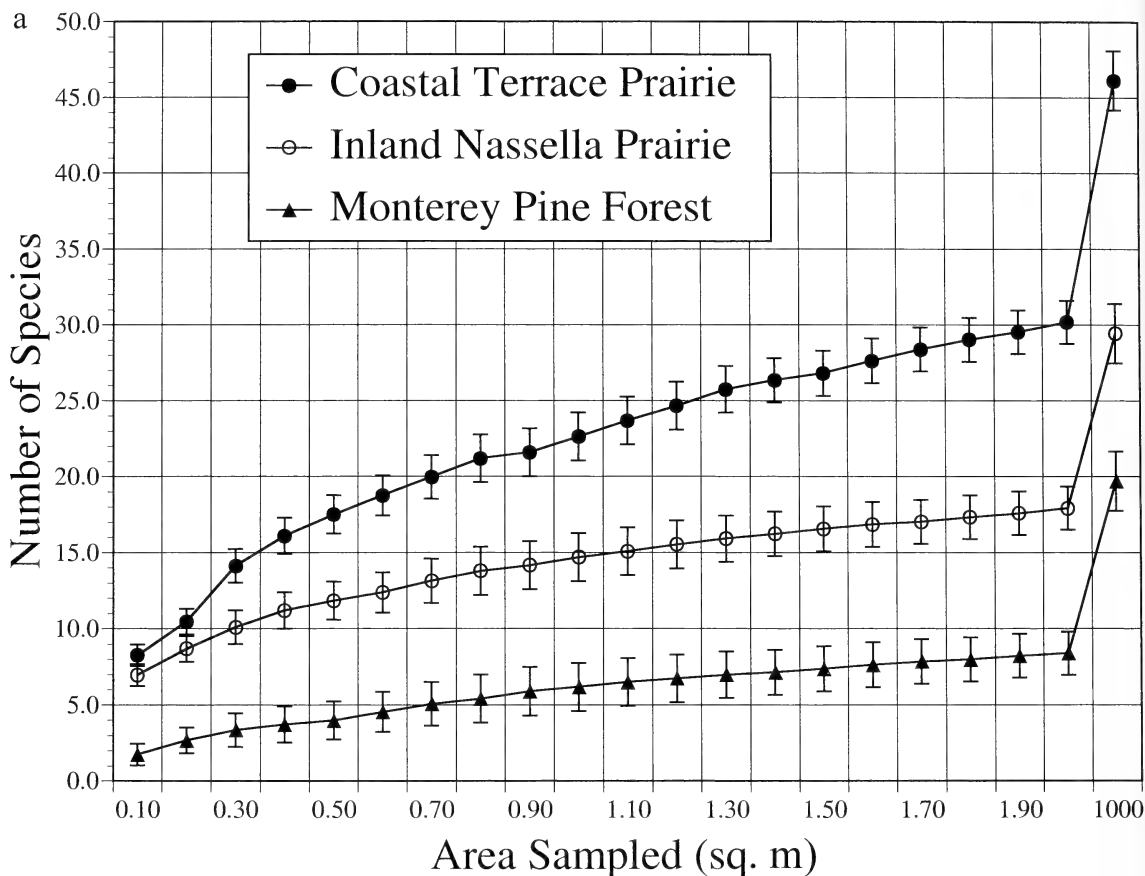
Fig. 2. a) Average number of species present as sampling areas are added in three coastal California plant communities, ±1 standard error.

(McBride and Heady 1968) or trees (e.g., *Pinus radiata* D. Don) (Callaway and Davis 1993) invade these coastal grasslands without fire or grazing. Pre-settlement fires in coastal grasslands were frequent, with 2–10 year return intervals (Greenlee and Langenheim 1990). Post-settlement disturbances have included year-round grazing by domestic livestock (Mack 1989). In most descriptions of coastal grasslands, *Nassella pulchra* is a co-dominant.

Native perennial grasslands persist along a continuum ranging from dominance by non-native species to being relatively free from exotics (Harrison et al. 2001). In this case, we examined species composition, invasibility, and diversity change along a gradient from central coast terraces inland to California's central coastal mountain ranges (here, the Sierra de Salinas). Our previous studies of the inland *Nassella* prairies investigated the role of gophers, grazing, and historic cultivation (Stromberg and Griffin 1996). Here, we extend our studies towards the coast to include grasslands that can be recognized as coastal terrace prairies by the constant presence of *Danthonia californica* and *Nassella*. We provide a background of data on the more

general discussion of patterns in species diversity (Tilman et al. 1997, Huston et al. 2000, Kaiser 2000) and the relationship between species diversity and invasive species (Symstad 2000) in landscape studies (Stohlgren et al. 1997).

STUDY AREAS

Thirty-three stands of coastal terrace prairie were sampled, from Avila Beach, north along the Big Sur coast to Pebble Beach and then north from Santa Cruz to San Bruno Mountain near San Francisco (Fig. 1). Stands were selected based on previous extensive botanical surveys of central coastal California grasslands (Kephart 1993; Yadon 1995; Stromberg and Griffin 1996). Stands were not recently grazed or cultivated and were initially selected based on co-dominance of *Deschampsia* or *Danthonia*.

Data from other studies were discovered and used. In 1965 and 1966, 46 homogenous stands of Monterey pine (*Pinus radiata*) forests were sampled from Cambria to Año Nuevo (White 1966a, Vogl et al. 1988). In 1993, 141 homogenous stands of coastal scrub were sampled from San Simeon to
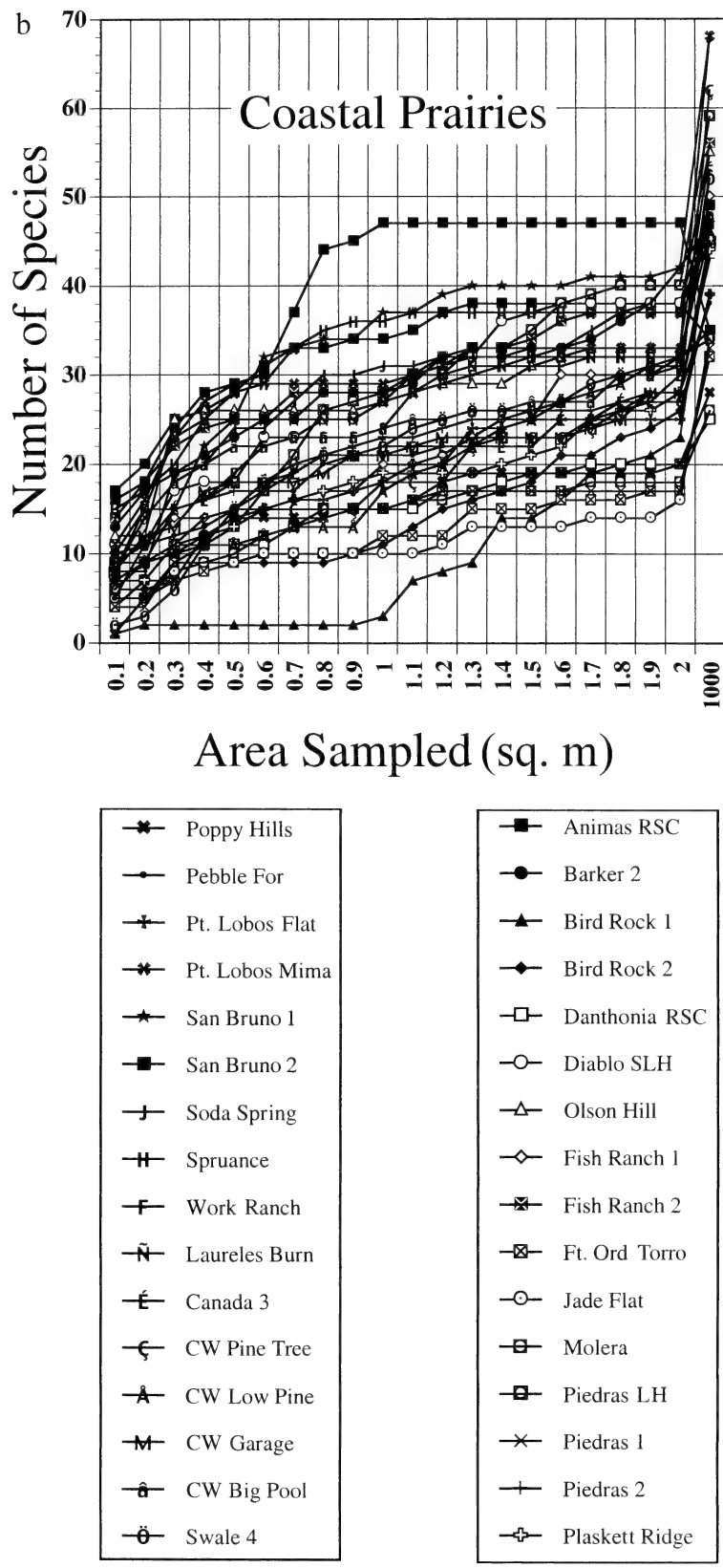
FIG. 2. Continued. b) Species/area curves for individual sampling localities.

Point Lobos (Heuer 1994). In 1991, 80 inland *Nassella* prairies in the Sierra de Salinas were sampled (Stromberg and Griffin 1996). Species richness depends on the scale of sampling (Gross et al. 2000) so comparisons to other studies were made at similar scales (1 sq. m).

METHODS

Sampling was done at the peak of the flowering season, from mid-April through May in 1996 and 1997. At each grassland stand (Fig. 1), we chose a homogenous area and flagged a 50 m × 20 m plot (0.1 ha) with the long axis parallel to topographic contours. We recorded presence of all plant species we could discover on the larger plots. Starting from the midpoint of the short axis, we placed steel quadrats (20 cm × 50 cm; 0.1 m²) at 2.5 m intervals along the 50 m midline of the 0.1 ha plot (20 quadrats/plot). For each quadrat, we recorded a cover class for canopy cover of all plant species we observed (Daubenmire 1959). Quadrats were painted to facilitate recognition of Daubenmire cover classes. A cover value of 0.01 was assigned to each species seen only in the larger plot and not seen in any smaller quadrat. Cover for each species at each stand (site) was calculated by averaging midpoints of the cover classes assigned to each of species in the 20 quadrats. Stands were at least 200 m apart, and more often, many kilometers apart. For each stand, we recorded aspect, elevation, distance inland from the coast, latitude and longitude (UTM), total number of plant species (Hickman 1993), soil type, land form, number of grasses and forbs, and numbers of perennials and annuals, native and exotic. Species were counted based on scores in successive quadrats on original field sheets; one coastal terrace data sheet was inadvertently lost after transcribing summary numbers so the species tally by area for one coastal terrace is missing. Nine soil series were included (Cook 1978; Ernstrom 1984). Land forms of coastal terrace prairies include: 1) coastal terraces immediately adjacent to the ocean that are almost level; 2) grasslands on the sides of isolated bald hills arising inland and up at least 10 m from the terraces, sometimes locally known as "potreros"; and 3) drier, inland ridges well over 100 m above the coastal terraces and bases of the inland mountain ranges. Staview 5.0 (SAS) was used for statistical comparisons. Bonferroni/Dunn post-hoc tests were included to show individual differences in pairwise comparisons (P = 0.05). We used several methods to order stands based on species composition and with regard to measures of diversity, including CCA, DCA and Bray-Curtis ordinations (PC-ORD ver 4) (ter Braak 1987a, b; McCune and Mefford 1999). Stand coordinates in our ordination were based on species data. We dropped species that occurred in only one stand with a cover value less than 5% in order to reach a numerical solution for CCA. Computational problems (Tausch et al. 1995) have been addressed, and the method we used is inherently robust (Leps and Hadincova 1992).

Species composition of the herb layer was observed using similar methods in 46 stands of Monterey pine forests. Discovery of archival records (K. White, unpublished data, Hastings archives) allowed us to include observations from 40 to 80 quadrats (20 cm × 50 cm; 0.1 m²) that were read as above for plant cover. A larger area of 0.1–1 ha was then searched for additional species present and each was recorded (K. White, unpublished data; Hastings archives).

Discovery of additional comparable data allowed us to include comparisons to coastal shrub communities (Heuer 1994). Coastal shrub communities, often adjacent to coastal terrace prairies, were sampled with 16 sq. m quadrats at 141 locations, again at the peak of the flowering season, in 1993. No larger sampling areas were surveyed for additional species (Heuer 1994) and only the larger (16 sq. m) quadrats were used.

Inland *Nassella* prairies were described in detail previously (Stromberg and Griffin 1996). We included inland prairies in this study to examine the larger scale differences across the landscape as inland *Nassella* prairies share *Nassella* and other species with coastal terrace prairies, but occur at a drier, inland part of an environmental continuum occupied by native grasslands in coastal California. Data sets from this study will be made available (ESA Ecological Archives or NRS archives).

RESULTS

Average species richness varies with the area sampled (Fig. 2). For individual sites, most reach an asymptote by about 2 m (Fig. 2a). No definitive asymptote is reached for the average coastal terrace prairie/Monterey pine forest (CTP) or (MPF). Species counts at 0.1 ha represents the best estimates for total species richness. Mean species numbers between all pairs are significantly different (paired t-tests, P < 0.001) for comparisons at 1 sq. m. and at 0.1 ha (Table 1).

This comparison of species richness with area leads to an interesting observation on the effects of a major human-directed use of the ecosystem. In a previous analysis of inland *Nassella* prairie stands with and without active grazing by domestic cattle, significantly fewer plant species were observed in grazed stands (Stromberg and Griffin 1996) based on areas of 0.1 ha. In this analysis of species number at a smaller sampling scale (1 sq. m), this pattern in species richness was reversed and is clearly dependent on scale (Fig. 2).

Coastal grasslands have much greater species richness in comparison to inland *Nassella* grasslands, coastal pine, or coastal scrub plant communities. A total of 82 species of grasses or sedges and 258 species of forbs (340 total) were found in

TABLE 1. COMPARISONS OF SPECIES DIVERSITY BETWEEN COASTAL TERRACE PRAIRIES (CTP), INLAND *NASSELLA* PRAIRIES (INP) AND MONTEREY PINE FORESTS (MPF) BASED ON FIRST TEN 0.1 SQ. M OBSERVATIONS (1 SQ. M) IN EACH SAMPLE. Coastal scrub species density was derived from 16 sq. m. quadrats at each stand, expressed here as species/sq. meter using $S = cA^z$ where $z = 0.25$.

Number of species per square meter	Count	Mean	Std. err.	
Coastal Terrace Prairies	32	22.6	1.58	
Inland *Nassella* Prairies	80	14.7	0.78	
Monterey Pine Forests	46	6.2	0.58	
Coastal Scrub	141	5.5	0.20	
Comparison of means (INP, CTP, MPF)	DF	Mean square	F value	P-value
Category	2	2615.2	62.9	<0.0001
Residual	155	41.6		

33 coastal terrace prairie stands. In 80 inland *Nassella* prairie stands, a total of 194 species were found; 136 plant species were found in 48 coastal Monterey pine stands (Vogl et al. 1988). Many fewer plant species (65 total) were found in 141 coastal scrub stands. Species richness (species/sq. m) in coastal prairies is about 3.5 times greater than in adjacent Monterey pine forests (Table 1) and nearly 4 times greater than in adjacent coastal scrub. Coastal prairies also have a much greater species richness compared to other grasslands in California and North America (Table 2) when each is presented at a comparable scale (1 sq. m).

Preliminary Bray-Curtis ordinations of the 33 stands revealed that both stands at Bird Rock and both forest stands in Pebble Beach (Poppy Hills, 24 Padre Lane-Table 4) were outliers. Although eliminated, they offer insights to dynamics of coastal prairies. Samples at Bird Rock had unusually high cover of *Carex pansa* L. Bailey (68% and 18%, respectively). *Carex pansa* was only found in two other stands, and there it was not abundant (cover
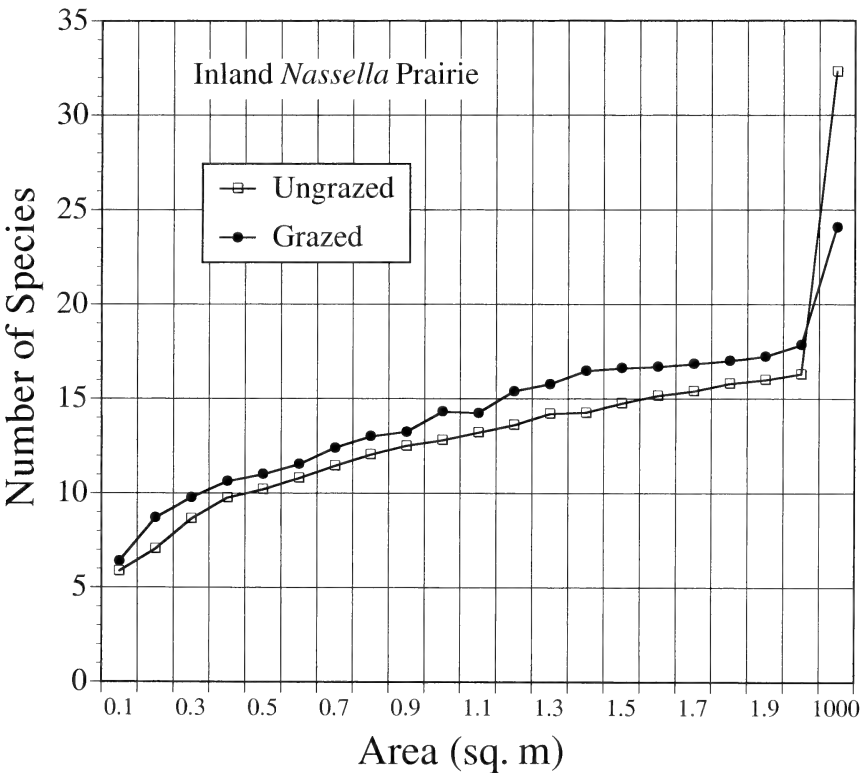
FIG. 3. Average number of species present as sampling areas are added in 43 ungrazed (1937–1991) inland *Nassella* prairies and 37 grazed (1880–1991) inland *Nassella* prairies (Stromberg and Griffin 1996).

TABLE 2. COMPARISON OF SPECIES RICHNESS (SPECIES/SQ. M, ± SD OR ± SE) IN CALIFORNIA GRASSLANDS AND OTHER ARID WESTERN PLANT COMMUNITIES. Species codes: Agr spi, *Agropyron spicatum*; Agr smi, *Agropyron smithii*; Amo can, *Amorpha canescens*; Art tri, *Artemesia tridentata*; Fes ida, *Festuca idahoensis Elmer*; Sti let, *Stipa lettermanii*; Poa pra, *Poa pratensis*.

Community name	Species density	Reference
Coastal Terrace Prairies	22.62, ± 8.9	This study.
Napa Co.–L. Berryessa, CA Serpentine Meadows	12.3, ± 2.3	(Harrison 1999)
Napa Co.–L. Berryessa, CA Non-Serpentine Meadows	10.3, ± 2.2	(Harrison 1999)
Monterey Co., Sierra de Salinas, CA Annual Calif. Grassland	14.7, ± 0.7	(Stromberg and Griffin 1996)
Bighorn Basin, C. WY Agr spi/Art tri	10.2, ± 0.5	(Stohlgren et al. 1999a)
Grant Teton, NW WY Agr spi/Art tri	8.9, ± 0.6	(Stohlgren et al. 1999a)
Gunnison, W. CO Sti let/Art tri	8.8, ± 0.4	(Stohlgren et al. 1999a)
Wind Cave, W. SD Poa pra/Amo can	8.7, ± 0.5	(Stohlgren et al. 1999a)
Charles Russell NWR, E. MT Agr smi/Art tri	4.6, ± 0.5	(Stohlgren et al. 1999a)
Yellowstone, W. WY Fes ida/Art tri	9.0, ± 0.6	(Stohlgren et al. 1999a)
Pipestone N.M., S. MN Tallgrass Prairie	12.2, ± 0.7	(Stohlgren et al. 1999b)
Cheyenne, SE. WY Mixed-grass Prairie	10.7, ± 0.5	(Stohlgren et al. 1999b)
Pawnee Butte, NE CO Short-grass Prairie	8.5, ± 0.4	(Stohlgren et al. 1999b)

<5%). Bird Rock 2 was the only stand to have more than 10% *Lolium multiflorum* Lam. with 34.4%. Padre Lane was the only stand where we found *Phalaris californica* Hook & Arn. and *Hierochloë occidentalis* Buckley and was one of only two stands with *Pinus radiata* (11%). Poppy Hills also had some *Pinus radiata* (2%), but was the only stand with *Rubus ursinus* Cham. & Schldl. or to have >1% *Arctostaphylos hookeri* G. Don (10%). Because these four stands have such exceptional composition, they confound analysis of the other open coastal prairies and were subsequently dropped from more detailed analysis of coastal terrace prairies.

Ordinations of species composition data from the 29 coastal terrace prairies showed that different land forms ("inland ridges," "coastal terraces," and "bald hills" above coastal terraces) each have a relatively distinct species composition. This was supported by results of the analysis of variance for individual measures. Comparisons of the three land forms of coastal terrace prairies showed that bald hills have more species of grasses and sedges overall (Table 3-a), more native grasses and sedges (Table 3-b) and more native forbs at both scales of sampling (Table 3-c, d) and so more species of native plants overall (Table 3-e). The cover of the native plants show a similar pattern—Bald Hills has more cover of natives (Table 3-f), particularly more cover of native perennial forbs (Table 3-g). Inland

ridges, as will be seen in a pattern extending to inland *Nassella* prairies (below) show more dominance by annual exotic forbs (Table 3-h) and other exotics in general (Table 3-i) than the more diverse, bald hill coastal terrace prairie.

Both inland *Nassella* prairies and coastal terrace prairies show an increase in the number of native species with total species richness in 0.1 ha plots (Figure 6-a, b). The number of exotic species also increases with species richness in inland *Nassella* prairies but not in coastal terrace prairies (Figure 6-c, d). The relative cover of exotics decreases in both inland *Nassella* prairies and coastal terrace prairies with species richness (Fig. 6-e, f). One relative outlier (Fig. 6-f) is instructive. This stand, Piedras Blancas-1, is unusually low in both relative cover of exotics and species richness because it is the only stand with 95% cover of one native, the perennial grass (*Deschampsia cespitosa* var. *holciformis*). In some cases then, relative cover of exotics can be low (~1%) even with low species richness (~34) if the total cover of the site is high. Including all coastal terrace prairies and inland *Nassella* prairies, species richness (0.1 ha) and total cover were positively correlated ($R^2_{adj} = 0.18$, F = 24.8, P < 0.001, residual df = 107) and relative cover of exotic species is negatively correlated with total cover ($R^2_{adj} = 0.19$, F = 25.6, P < 0.001, residual df = 107). Native species richness (0.1 ha) and exotic species richness were positively corre-

TABLE 3. BASED ON OPEN COASTAL GRASSLANDS, DIFFERENCES BETWEEN MEAN VALUES FROM COASTAL TERRACES (CT, N = 10), COASTAL BALD HILLS (BH, N = 10 AND INTERIOR DRY RIDGES (IR, N = 9) ARE SHOWN BASED ON ANALYSIS OF VARIANCE. Bonferroni/Dunn post-hoc comparison (e.g. BH, CT) are shown only with a significance level of 0.05. Residual df = 26 in all 2-way ANOVA. Arcsin-square root transformation of ratio data were done before ANOVA; results expressed below in ratios.

a. Species of Grasses and Sedges 0.1 ha
   F = 3.61, P = 0.04

	mean	std. error	
CT	14.5	1.2	
BH	15.4	1.4	BH, IR P ≤ 0.05
IR	11.0	0.8	

b. Species of Native Grasses and Sedges 2 sq. m
   F = 6.1, P = 0.006

	mean	std. error	
CT	14.5	1.2	
BH	15.4	1.4	BH, IR P ≤ 0.05
IR	11.0	0.8	

c. Species of Native Forbs 0.1 ha
   F = 3.92, P = 0.032

	mean	std. error	
CT	17.6	2.6	
BH	28.9	3.4	BH, CT P ≤ 0.05
IR	20.4	3.0	

d. Species of Native Forbs 2 sq. m
   F = 3.45, P = 0.04

	mean	std. error	
CT	9.7	1.9	
BH	17.1	2.3	BH, CT P ≤ 0.05
IR	13.4	1.9	

e. Species of Native Plants 0.1 ha
   F = 4.39, P = 0.02

	mean	std. error	
CT	25.1	2.9	
BH	36.7	3.8	BH, IR P ≤ 0.05
IR	24.6	2.9	

f. Cover—Native Plants
   F = 7.02, P = 0.036

	mean	std. error	
CT	67.7	8.8	CT, IR P ≤ 0.01
BH	77.7	5.3	BH, IR P < 0.01
IR	42.9	4.6	

g. Cover—Native Perennial Forbs
   F = 3.89, P = 0.035

	mean	std. error	
CT	12.2	2.7	
BH	21.4	4.7	BH, IR P ≤ 0.05
IR	8.6	1.6	

h. Cover—Annual Exotic Forbs
   F = 6.84, P = 0.004

	mean	std. error	
CT	9.7	2.3	CT, IR P ≤ 0.05
BH	6.9	1.7	BH, IR P ≤ 0.05
IR	20.6	3.9	

i. Ratio of Exotic Species/Total Forb Cover
   F = 4.86, P = 0.016

	mean	std. error	
CT	0.48	0.069	
BH	0.37	0.048	BH, IR P < 0.05
IR	0.63	0.025	

lated for inland *Nassella* prairies (R^2_{adj} = 0.23, F = 24.6, P < 0.001, residual df = 78) but not for coastal terrace prairies (R^2 = 0.02, F = 0.67, P < 0.001, residual df = 27).

Considering just the 29 open coastal terrace prairies, grasses and forbs differ in how they vary with species richness at 0.1 ha. On this scale, neither total vegetative cover nor cover of native species is related to species richness. However, cover of all exotic species decreases significantly with increasing species richness (R^2_{adj} = 0.15, F = 6.0, P < 0.05, residual df = 27). This decrease in cover of exotics with an increase in species richness was largely due to the decrease in cover of exotic grasses. Cover of exotic grass was significantly negatively correlated with species richness (R^2_{adj} = 0.12, F = 4.96, P < 0.05, residual df = 27). Neither the cover of exotic forbs or the number of exotic forbs was correlated with species richness in coastal terrace prairies. The degree to which the grasses are native increases with species richness; the number of native grasses is correlated with species richness (R^2_{adj} = 0.14, F = 5.56, P < 0.05, residual df = 27) although the cover of native grass is not correlated. The degree to which forbs are native also increases with increasing species richness. In this case both cover and number of native forbs (0.1 ha) were significantly correlated with species richness (respectively, R^2_{adj} = 0.29, F = 12.9, P < 0.001, residual df = 27 and R^2_{adj} = 0.83, F = 136, P < 0.001, residual df = 27).

The summary of the 25 most frequent and dominant species of grasses and sedges in the coastal prairies (Fig. 4) reveals that coastal prairies are heavily invaded with non-natives. The widespread fescue, *Vulpia* spp. is in most samples and is often very abundant. *Danthonia californica, Nassella pulchra,* and *Festuca rubra* are the native grasses that define this community. A summary of the 25 most frequent and dominant species of forbs in coastal prairies (Fig. 5) show a similar dominance by non-natives; in this case by widespread *Plantago, Erodium,* and *Hypochaeris,* all of which extend well inland. Most important natives include the very similar *Plantago erecta* E. Morris and *Baccharis pilularis.* These natives, along with *Viola, Sidalcea, Cammisonia,* and *Acaena* are the native forbs that complete the definition of these coastal prairies. In this community, the dominance of grasses drops off rapidly (Fig. 4), while the cover and frequency of the forbs is far greater for more species (Fig. 5).

Dominance of exotic grasses and forbs in coastal terrace prairie increases inland coastal terraces, to bald hills, and further to the drier ridges (Table 3). For coastal prairies, the average ratio of the number of exotic grass or sedge species to total species present is 0.44, and the average ratio of exotic forb species is 0.33 (n = 33). Corresponding average ratios of exotic species in inland *Nassella* prairies are 0.79 and 0.19 (n = 80).

TABLE 4. STAND NAMES AND LOCATIONS (UTM) INCLUDED IN SAMPLING OF CALIFORNIA COASTAL GRASSLANDS.

No.	Stand name	Abbreviation	East	North	Soil type
1.	Barker Ranch, Laureles Ridge	Barker 1	614.291	4041.710	Sandy Loam
2.	Barker Ranch, Laureles Ridge	Barker 2	613.835	4041.865	Sandy Loam
3.	Bird Rock, Inland terrace	Bird Rock 1	593.202	4050.157	Sand
4.	Bird Rock, Inland terrace	Bird Rock 2	593.177	4050.126	Sand
5.	Canada Woods Site No. 4	CW No. 4	603.776	4051.868	Clay Loam
6.	Canada Woods, Garage Site	CW Garage	604.100	4047.500	Clay Loam
7.	Canada Woods, Lower Pine Tree	CW Low Pine	603.500	4048.200	Clay Loam
8.	Canada Woods, Pine Tree	CW Pine Tree	606.660	4049.100	Clay Loam
9.	Canada Woods, Swale	CW Swale	603.800	4046.900	Clay Loam
10.	Canada Woods, Big Pool	CW Big Pool	604.085	4046.295	Clay Loam
11.	Fish Ranch, above Entrance Rd.	Fish Ranch 1	597.300	4042.694	Silty Loam
12.	Fish Ranch, above Entrance Rd.	Fish Ranch 2	597.313	4042.692	Silt Loam
13.	Fort Ord, opposite Toro Park	Ft. Ord Toro	615.941	4052.110	Sandy Loam
14.	Jade Flat, Central Terrace	Jade Flat	638.283	3975.370	Serpentine Clay
15.	Laureles Grade, Laureles Ridge	Laureles	611.870	4043.319	Sandy Loam
16.	Molera State Park, N. Terrance	Molera	602.546	4016.610	Sand Loam
17.	Olson Hill, Diablo Canyon	Olson Hill	698.859	3896.149	Loam
18.	Pebble Beach, 24 Padre Lane	Pebble For	592.366	4048.055	Loamy Sand
19.	Plaskett Ridge, Above Camp	Plaskett Rdg	638.277	3975.359	Serpentine Rock
20.	Point Lobos, Escobar Flat	Pt. Lobos Flat	597.250	4042.194	Sandy Loam
21.	Point Lobos, Mima Mounds	Pt. Lobos Mima	584.700	4041.300	Clay Loam
22.	Poppy Hills, Opposite Golf Club	Poppy Hills	595.225	4048.980	Sandy Loam
23.	Pt. Piedras Blancas Light House	Piedras LH	646.262	3948.422	Sand
24.	Pt. Piedras Blancas Terrace 1	Piedras 1	654.425	3951.349	Loam
25.	Pt. Piedras Blancas Terrace 2	Piedras 2	654.347	3951.341	Loam
26.	Rancho San Carlos, Animas Entr.	Danthonia RSC	600.086	4040.213	Clay Loam
27.	Rancho San Carlos, Animas Rdg.	Animas RSC	600.071	4041.197	Clay Loam
28.	San Bruno Mtn., Great Meadow	San Bruno 1	548.059	4171.974	Loamy Sand
29.	San Bruno Mtn., Great Meadow	San Bruno 2	549.274	4171.733	Loamy Sand
30.	San Louis Hill, Diablo Canyon	San Luis Hill	703.599	3893.915	Clay Loam
31.	Soda Springs, Bluff W. of Hwy 1	Soda Spring	646.266	3965.330	Serpentine Rock
32.	Spruance Meadow, Spruance Dr.	Spruance	595.662	4047.953	Loamy Sand
33.	Work Ranch, Hwy 68	Work Ranch	603.586	4048.821	Sandy Loam

We used CCA to sort out which individual comparisons of community characteristics (measures of diversity and the degree of invasion by exotic species) are most closely associated with vegetation composition across the landscape gradient from inland *Nassella* prairies to coastal terrace prairies. Some of these measures were highly correlated, so we proceeded with only 19 (Table 5). Plant species with total cover of less than 0.05% and which occurred in 5 or fewer stands were eliminated, leaving 192 species. With these simplifications (tolerance set to 0.100000E-12), PCord reached a CCA solution after fewer than 100 iterations. Inland *Nassella* prairies were clearly grouped to the left (Fig. 7) and coastal terrace prairies were on the right. The highest "intraset correlation" (ter Braak and Smilauer 1998) with this first axis was the cover of native, perennial grass and on the second axis, the cover of exotic species (Fig. 7). Coastal terrace prairies are characterized as having both more species and higher cover of native perennial grasses than any of the tightly grouped (thus similar) inland *Nassella* prairies that are clearly placed to the left of the first axis where stands can be described as having higher cover of annual, exotic forbs (for example, *Erodium cicutarium* (L.) L. Hér). The second axis distinguishes between coastal terrace prairies into those with relatively more dominance by exotic species (Piedras Blancas Light House, Fish Ranch, etc.) and those with relatively high cover of native, perennial forbs (San Bruno, Soda Springs, Piedras Blancas 1, etc.) (Fig. 7—joint plot).

By restricting our focus to only coastal terrace prairies, we can examine the pattern of species composition and floristic characteristics at a smaller scale. By dropping the 80 inland *Nassella* prairies, the number of plant species (total cover >0.5%) included in the CCA dropped to 149. Correspondingly, more of the floristic variables were highly correlated (Table 5) and only 12 were relatively independent. A joint plot (Fig. 8) shows many coastal terrace prairies in a group with relatively high cover of exotic species. The highest intra-set correlation with the first axis was with cover of exotic species. The highest intra-set correlation with the second axis was with the number of native forbs. Stands such as San Bruno, Soda Springs, the stands near Avila Beach (Olson Hill, San Luis Hill) are exemplary coastal terrace prairies with fewer exotics and higher cover of native forbs. The Point Lobos Mima mound prairie and Piedras Blancas 1 are coastal terrace prairies with fewer exotics, higher

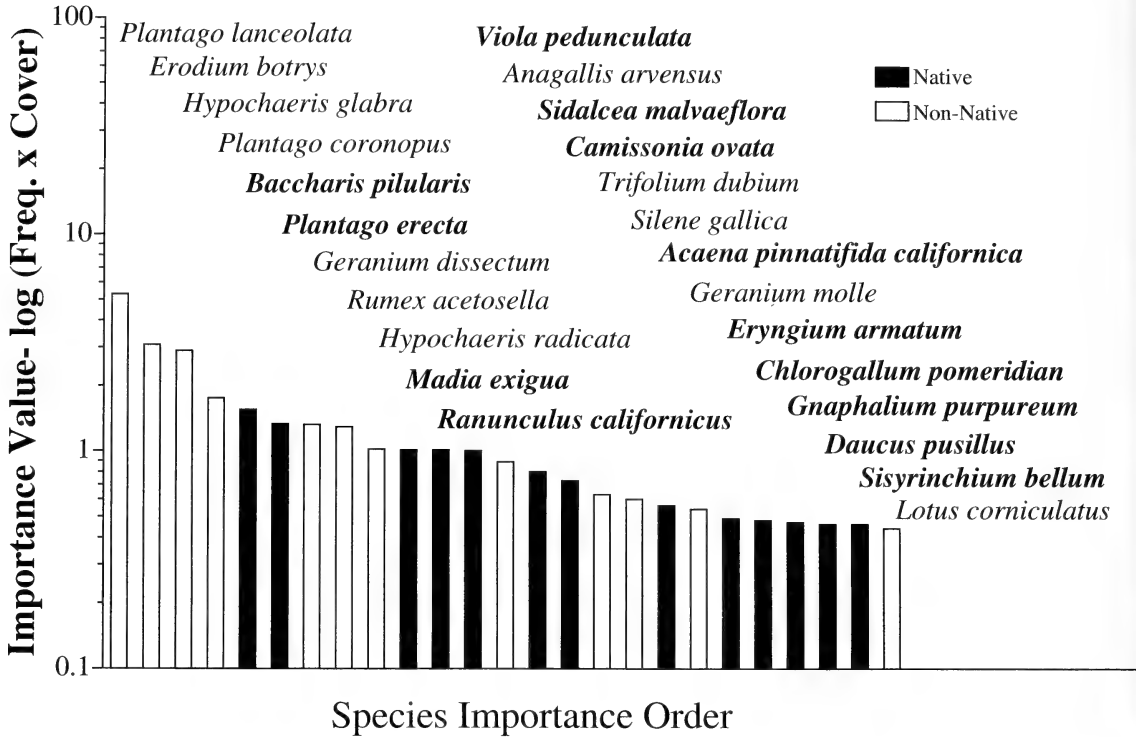## Dominant Grasses/Sedges - Coastal Grasslands
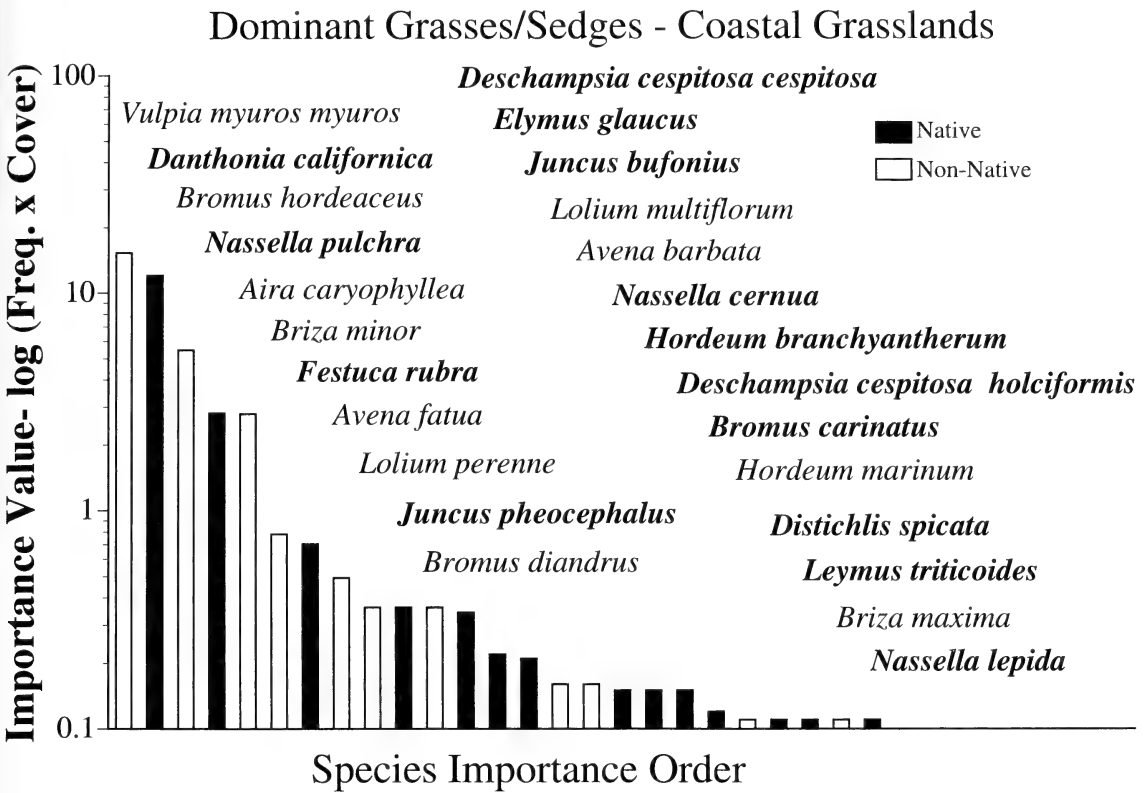
FIG. 4. Importance value (frequency × average percent cover) of the 25 most dominant species of grasses and sedges, averaged from 29 coastal terrace prairies in central, coastal California.

cover of native forbs and more native grasses (Fig. 8—joint plot) while stands clustered on the left side relatively more cover of exotic species.

Soils and locations of the various sites are described in Table 4. Fourteen of the coastal terrace prairies (44%) occurred on soils with a hardpan from 10–20 cm beneath the surface. An additional three coastal terrace prairies occurred on serpentine rock or clay with limited drainage. A hardpan that provides standing water during the winters was often present, but apparently not required. Coastal terrace prairies also occurred on sands, loams and clays.

DISCUSSION

Diversity of plant species in coastal terrace prairies is among the highest in grasslands of North America (Stohlgren et al. 1999b). County and wildland planners often have selected coastal terrace prairies for development, perhaps not recognizing the biodiversity of coastal terrace prairies or because political support to protect forests or coastal scrub has been comparatively well organized. If protection of biodiversity is a goal, then coastal terrace prairies should be protected and development should be focused on relatively species-poor plant communities.

Invasions of natural communities by exotic spe-

cies may occur more readily in areas of low species diversity than in areas of high species diversity (Darwin 1859). Plant communities with low species diversity (and total cover) may use resources less completely, allowing invasion by similar species (MacArthur and Wilson 1967; Pimm 1991; Tilman et al. 1997). Evidence for this relationship between diversity and invasions in grasslands depends on scale, and at a landscape scale, may be reversed (Stohlgren et al. 1999b). Based on the number of species, our studies do not support the theory that exotics are more abundant where species diversity is relatively low; inland *Nassella* prairies (but not coastal terrace prairies) with the highest diversity have more exotic species (Fig. 6c, d). But, numbers of species probably do not reflect ecosystem function. Species occupying more space intercept more light, and presumably are more important in nutrient capture and storage. In both inland *Nassella* prairies and coastal terrace prairies, most species in our grasslands have cover <5%. Two species may be equally counted as present, but one may occupy far more cover in the community. Based on relative cover (Figs. 6e, f, 7) both diverse inland *Nassella* prairies and coastal terrace prairies have reduced exotic dominance, supporting the theory that less diverse communities are more likely to be invaded.

Ordinations of the species and stands agree with

Dominant Forbs - Coastal Grasslands

FIG. 5. Importance value (frequency × average percent cover) of the 25 most dominant species of forbs, averaged from 29 coastal terrace prairies in central, coastal California.

our general understanding of the biology of individual species. The ordinations are also consistent with patterns seen by making pairwise statistical comparisons (Table 3, Fig. 7). All coastal terrace prairies have been invaded to some degree by exotics, but the importance of exotic species is far greater in inland *Nassella* prairies. Two of the three grasses with the most cover (Fig. 4) and the four forbs with the most cover in coastal terrace prairies are exotics (Fig. 5).

Although the effects of grazing by large domestic herbivores on these grasslands were not specifically addressed, a re-analysis of inland *Nassella* prairie data at various scales of sampling (Figs. 2, 3) supports observations elsewhere that the loss in plant species diversity in grasslands grazed by herbivores is only seen at a scale larger than about 100 m² (Chaneton and Facelli 1991, Olff and Ritchie 1998). Grazing, or its removal, probably has little effect on species diversity in other California grasslands because grazing has been continuous for centuries following European settlement (Harrison 1999). At some scales, grazing may have little effect on native species richness in other North American grasslands (Stohlgren et al. 1999a). All grasslands in this study were probably grazed since European settlement. There is no evidence that herds of large herbivores co-evolved with the California coastal grasslands (Painter 1995). In general, domestic livestock grazing has had severe impacts on grassland ecosystems in western North America (Painter and Belsky 1993) and livestock removal has been suggested at various scales (Bock et al. 1993). However, grazing has been present for so long that careful consideration must be given before livestock are removed from coastal grasslands. On Santa Cruz Island, grasslands formerly grazed by cattle now support near monocultures of *Foeniculum vulgare* Miller, an exotic plant formerly held in check by year-long grazing (M. Stromberg pers. obs., Mayfield et al. 2000). On other coastal parklands where grazing has been entirely removed after many years of year-round grazing (Andrew Molera State Park, Santa Clara County Parks, San Mateo County's Mid-Peninsula Open Space District) we have seen extensive, rapid expansions of *F. vulgare, B. pilularis,* and *Dipsacus* spp. where these plants were formerly relatively unimportant.

Most coastal terrace prairies were clearly open grasslands, but the composition of several stands included trees and shrubs (e.g., Poppy Hills, Padre Lane). The presence of otherwise typical coastal terrace prairies grasses and forbs in these brushy or
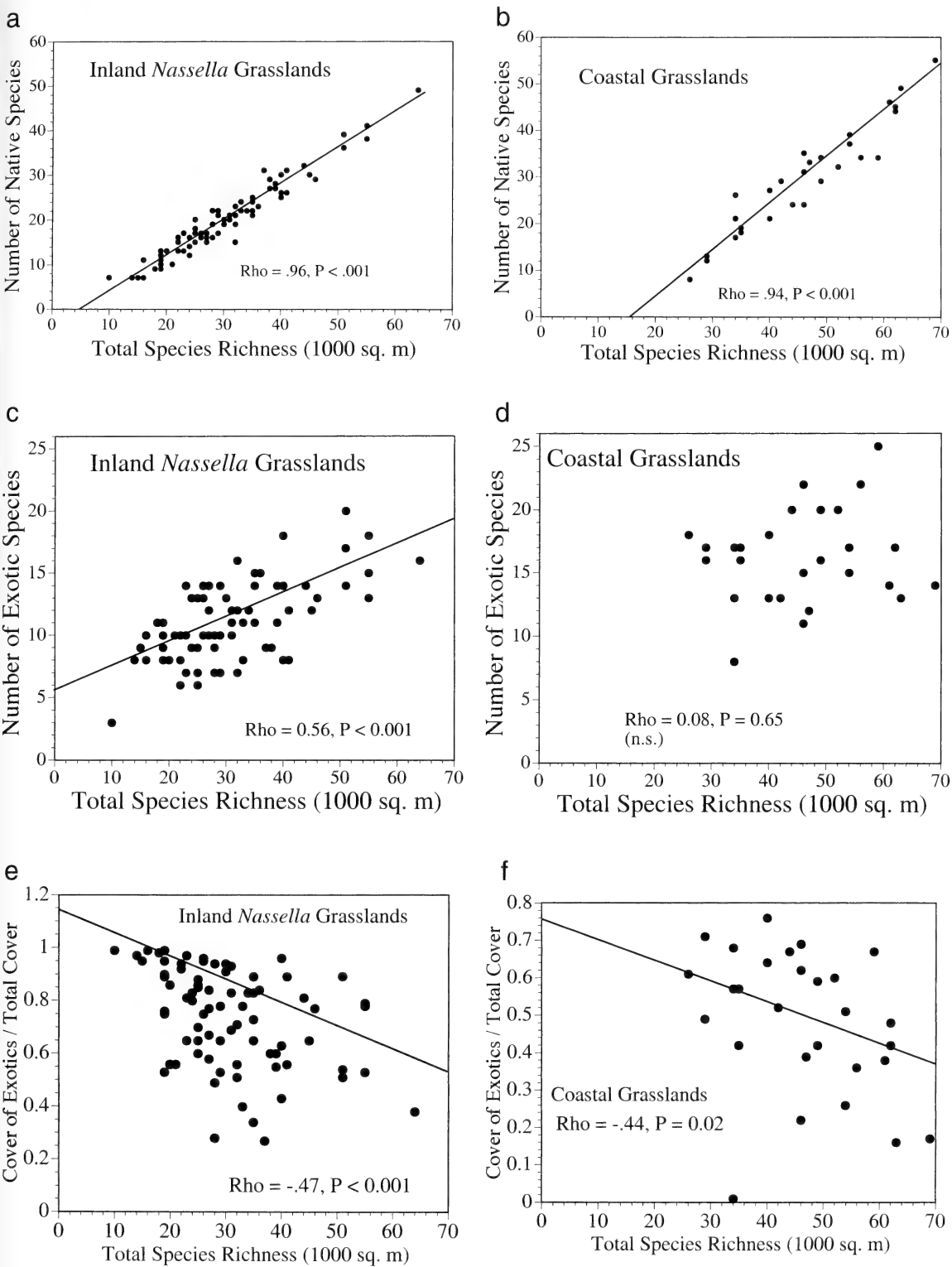
FIG. 6. Spearman rank correlation between species richness and number of all native plant species for a.) 80 inland *Nassella* prairies and b.) 29 coastal terrace prairies. Spearman rank correlation between species richness and number of all exotic plant species for c.) 80 inland *Nassella* prairies and d.) 29 coastal terrace prairies. c. Spearman rank correlation between species richness and relative cover of exotic plant species for e.) 80 inland *Nassella* prairies and f.) 29 coastal terrace prairies.

TABLE 5. FLORISTIC VARIABLES CONSIDERED IN ANALYSIS OF SPECIES RICHNESS IN CALIFORNIA GRASSLANDS. Highly correlated variables were dropped, leaving 19 variables (middle column) with sufficiently minimal correlation required to compute canonical correlation analysis (Fig. 6). When only 29 coastal terrace prairies are compared, 12 floristic variables were included in the analysis (Fig. 7). For example, in a CCA including 80 INP and 29 CTP, variable 1 (No. of Species in 2 sq. m) was dropped as it had a high correlation with variable 21 (No. of all Natives).

		Correlated variable(s) no., R^2	
No.	Variable name	80 INP and 29 CTP	29 CTP
1.	No. of Species in 2 sq. m	21, .94	21, .92
2.	No. of Species in 0.1 ha	25, .87	25, .91; 27, .95
3.	Total Vegetative Cover	included	included
4.	Cover of all Exotics	included	included
5.	Cover of all Natives	8, .78; 17, .79; 6, .86	6, .80
6.	Cover of Native, Perennial Grass	included	included
7.	Cover of Native, Perennial Forbs	included	included
8.	No. of Native, Perennial Grasses (0.1 ha)	17, .92; 23, .99	23, .99
9.	No. of Native, Perennial Forbs (0.1 ha)	included	25, .91
10.	Cover of all Exotic Grasses (0.1 ha)	included	4, .91
11.	Cover of all Exotic Forbs (0.1 ha)	included	included
12.	Cover of Annual, Exotic Grasses	4, .99	4, .90
13.	No. of Annual, Exotic Grasses (0.1 ha)	included	16, .84; 22, .94
14.	Cover of Annual, Exotic Forbs	included	included
15.	No. of Annual, Exotic Forbs (0.1 ha)	included	24, .92
16.	No. of Exotic Grasses (2 sq. m)	included	22, .88
17.	No. of Native Grasses (2 sq. m)	8, .94	8, 82; 23, .87
18.	No. of Exotic Forbs (2 sq. m)	included	20, .86
19.	No. of Native Forbs (2 sq. m)	included	included
20.	No. of all Exotics (2 sq. m)	included	included
21.	No. of all Natives (2 sq. m)	included	included
22.	No. of all Exotic Grasses (0.1 ha)	13, .96	13, .94
23.	No. of all Native Grasses (0.1 ha)	included	included
24.	No. of all Exotic Forbs (0.1 ha)	included	26, .86
25.	No. of all Native Forbs (0.1 ha)	included	included
26.	No. of all Exotics (0.1 ha)	included	included
27.	No. of all Natives (0.1 ha)	25, .94	25, .95
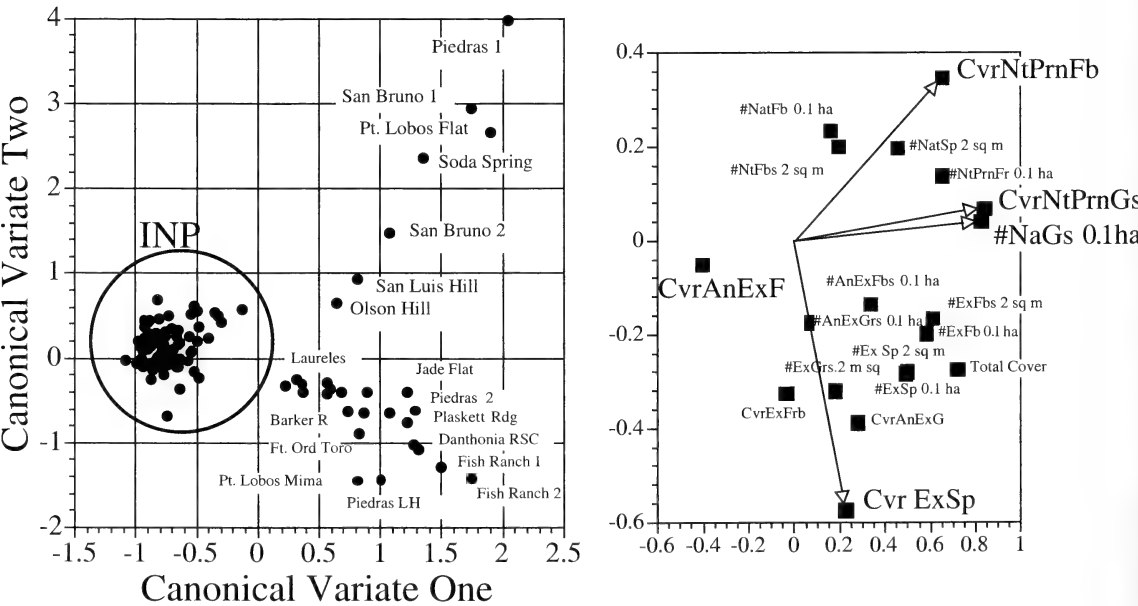
FIG. 7. Canonical correspondence analysis (ter Braak 1994) of 80 inland *Nassella* prairies and 29 coastal terrace prairies, based on cover of 197 plant species and 19 floristic variables. Inset: joint plot of stands and correlated floristic variables for all stands; length of vector associated with each variable is related to correlation with position of stand on canonical axes; highly correlated floristic variables are plotted near each other.
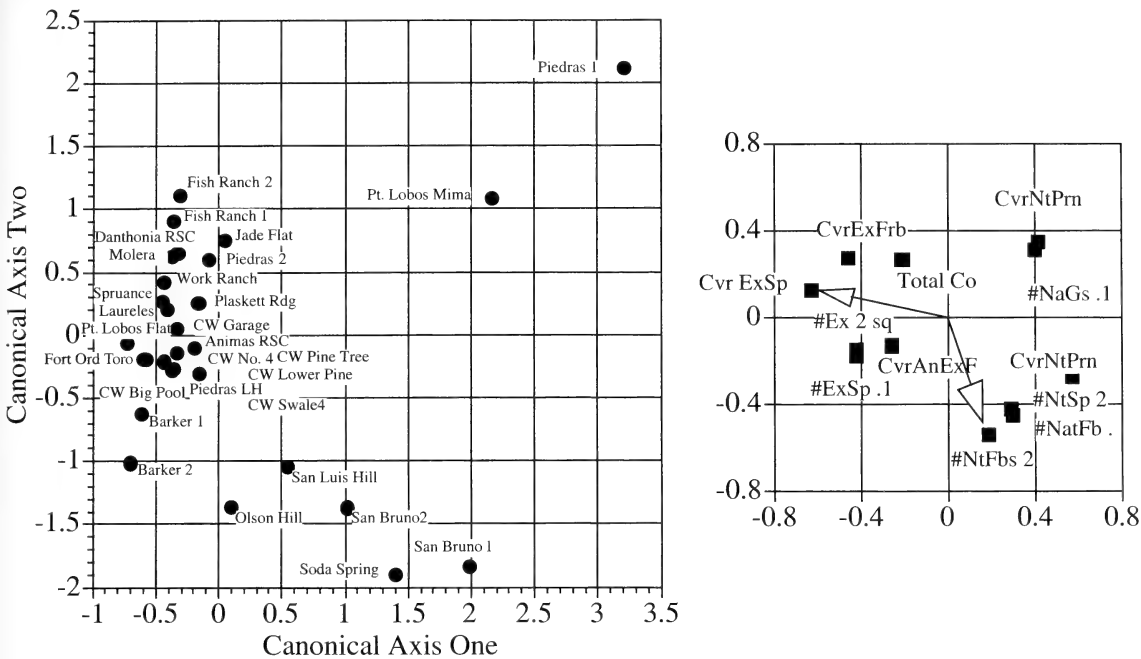
FIG. 8. Canonical correspondence analysis of 29 coastal terrace prairies based on cover of 149 plant species and 12 floristic variables. Inset: joint plot of floristic variables for axes one and two.

forested stands supports the concept of a dynamic tension between forest and grassland vegetation mediated by occasional fire (or grazing) in the coastal communities (Greenlee and Langenheim 1990). Currently, central California coastal grasslands are gradually seeing increased dominance by the native coastal shrub (*B. pilularis*) (McBride and Heady 1968) or oak woodland (Callaway and Davis 1993). Indeed, *B. pilularis* is a co-dominant native of the coastal prairies.

California's human population will double by 2040, and coastal development is much faster than that in interior California (Medvitz and Sokolov 1995). Although prescribed fires are the most cost-effective way to maintain the grasslands on a large scale (Kephart 2000), current and planned development almost precludes this option. Small-scale prescribed burns, mowing, and controlled grazing during the dry season should be included in management strategies to sustain the long-term viability of California's coastal prairies.

Although some may attempt to assign names or define units of vegetation (Sawyer and Keeler-Wolf 1995) this may be impossible (Zedler 1997) because vegetation occurs on a continuum in the environment where each species has an individual distribution on the gradient from coastal to inland. Even if we could find identical environments, species composition would probably vary due to other factors that have undoubtedly influenced the abundance of individual species in a given year (Fox and Fox 1986). Gradients may also be based on

competition; from wet (coastal) to dry (inland) (Lane et al. 2000) or disturbance (fire frequency, grazing duration and intensity, gopher abundance, etc.).

Gopher tailings probably sustain a disturbance regime of inland California annual grasslands and old fields (Stromberg and Griffin 1996) where gopher density can be very high. On coastal terrace prairies, however, gopher tailings rarely observed.

We did not sample all known high-quality or relict stands in this study area. Terraces on the San Simeon Ranch, the grasslands just north of Santa Cruz adjacent to Wilder Ranch State Park, those on the San Mateo coast, and those north of Bodega Bay need more investigation.

Coastal prairies support a number of state or federally designated "rare" species and are often managed for protection of rare animals (Launer and Murphy 1994). Rare animals include several butterflies; the Mission Blue and San Bruno Elfin (McClintock et al. 1990, Weiss 1993). Conservation of the coastal terrace prairie on San Bruno Mountain includes the first "habitat conservation plan" approved by the federal government. Species considered as "special plants" by various regulatory agencies and observed in this study include: *Arctostaphylos hookeri* G. Don, *Astragalus tener* A. Gray var. *titi* (Eastw.) Barneby, *Allium hickmanii* Eastw. (in 23% of the coastal terraces sampled), *Sanicula maritima* S. Watson, *Trifolium polyodon* E. Greene, *Psilocarphus tenellus* Nutt. var. *globiferus* (DC.) Morefield, *Cirsium occidentale* (Nutt.)

Jepson var. *compactum* Hoover, *Perideridia gaird-neri* (Hook & Arn.) Mathias, and *Arabis blephar-ophylla* Hook & Arn. Each of these officially rare species occurred in only one stand, and then only sparsely in the larger plot (50 m × 20 m, 0.1 ha). We also found *Ophioglossum californicum* Prantl at Spruance Meadow, not seen in Monterey County since its original collection in 1910. *A. t.* var. *titi* is federally listed as endangered and occurs only in one location (Bird Rock). We purposely included this site in the sampling as it occurs on an exceptional relict stand including *Danthonia* and *Deschampsia cespitosa* var. *holciformus*. Land managers who can identify the species assemblages described here (Figs. 4, 5) should expect other associated rare species.

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PRE-AGRICULTURAL GRASSLAND IN CENTRAL CALIFORNIA

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Abstract

An increasingly dogmatic paradigm maintains that central California's pre-agricultural grasslands were once entirely dominated by the bunchgrass *Nassella pulchra*. Evidence from early records and current relict vegetation, however, indicates they were spatially diverse. In moderate precipitation areas *Nassella pulchra* frequently dominated grasslands in foothills and occasionally also on sandy valley floors, but grassland on heavier soils in valleys and on many hillslopes was dominated by the rhizomatous graminoids *Leymus triticoides, Carex barbarae,* and *C. praegracilis.* Dominance shifted to spring-active annual forbs in low precipitation areas and probably to summer-active annual forbs (tarweeds) on infertile old terrace soils.

Introduction

When I was seeking remnant examples of native perennial prairie in 1994 as models for grassland restoration in California's Central Valley, it soon became evident that there were at least an order of magnitude more remnants dominated by the rhizomatous native perennial grass *Leymus triticoides* (Buckley) Pilger than by native bunchgrasses like *Nassella pulchra* (A. Hitchc.) Barkworth. This observation was surprising since conventional botanical wisdom at that time assumed herbaceous valley vegetation was formerly dominated by bunchgrasses before nineteenth century land use changes caused their almost total replacement by exotic annual grasses (Heady 1977).

Examination of such apparent paradoxes has gradually led to a reevaluation of long-standing assumptions about the valley's original natural vegetation. In 1981, for example, two Madroño papers questioned the then generally accepted bunchgrass dominance paradigm (BDP). Bartolome and Gemmill (1981) first showed *N. pulchra* is not well-adapted for dominating pristine herbaceous vegetation. Then, three months later, Wester (1981) provided historical evidence that well before the post-1850 cattle introduction traditionally blamed for the demise of bunchgrasses, they were either rare or entirely absent in the San Joaquin Valley, a significant part of the area they were traditionally assumed to dominate.

The BDP remained one of California botany's most dominant paradigms through the 1990's, however, despite these and numerous other studies. Late in the decade Hamilton (1997) systematically demonstrated its creation was motivated by pre-existing theory rather than strong evidence, but it is too soon to determine if his work significantly impacted the surprisingly durable BDP. Meanwhile many California Floristic Province vegetation surveys uncritically claim its grasslands were once covered by bunchgrass prairies dominated by *N. pulchra* (Barbour and Christensen 1993; Schoenherr 1992; Sims

1988), while others treat the BDP with only mild scepticism and fail to suggest alternative hypotheses (Barbour et al. 1993). One excellent survey of the state's vegetation in that period (Holland and Keil 1989) acknowledged Wester's work and questioned BDP, but local publication limited its impact until a new edition (1995) was issued by a national publisher. California native grassland restoration efforts consequently still emphasize creating bunchgrass prairies even where their former presence is highly unlikely (Harker et al. 1993; Dremann 1995).

Evidence for BDP rests on Clements' (1920, 1934) observation of *N. pulchra* stands along railroads in the San Joaquin Valley near Fresno and his subsequent conclusion they were relicts of a formerly widespread bunchgrass prairie that once covered most California Floristic Province valleys and foothills. Hamilton (1997) amply demonstrated, however, that this conclusion was heavily influenced by and made to fit grassland theories Clements had previously developed outside California. As discussed above, Bartolome and Gemmill (1981) also demonstrated that *N. pulchra* is a semiruderal species adapted to disturbed fire-prone habitats like those seen by Clements along railroads because its abundant seeds can readily germinate on bare ground and thus permit rapid colonization of sites where disturbance has temporarily reduced competition from other species. Ironically Clements' BPD is alive and well even though his more famous climatic monoclimax theory from which it arose was discredited and subsequently discarded (Daubenmire 1968; Krebs 1972; Mueller-Dombois and Ellenberg 1974).

The fully developed BDP has several key assumptions:

1. "*Stipa* (= *N.*) *pulchra,* beyond all doubt, dominated the valley grassland" (Heady 1977).

2. Following Küchler (1964), the largest single area of former valley grassland in California included much of the Central Valley.

3. Replacement of native bunchgrasses by the ex-

otic annuals that presently dominate California grasslands started with overgrazing in the 1850's and accelerated during severe drought in the 1860's.

OBJECTIVES AND METHODS

To determine if BDP's assumptions are accurate I looked for evidence about the nature of central California's pre-agricultural grasslands in two places:

1. Historical accounts describing central California grassland during the period their domination by bunchgrasses was assumed by BDP.

2. Vegetation surveys of central California grassland areas dominated by native species. These started along the Cosumnes River in southern Sacramento County where my interest in the BDP problem began but ultimately included several other areas of interest. Each survey consisted of a sample stand (relevé) in essentially homogeneous vegetation and used Braun-Blanquet's cover-abundance scale (Mueller-Dombois and Ellenberg 1974) to estimate cover of all vascular plant species in the stand. In the scale 5 = >75% cover, 4 = 50–75%, 3 = 25–50%, 2 = 5–25%, 1 = numerous but <5%, and + = few. The scale also includes r for solitary individuals but all such records were assigned to +.

RESULTS

Historical records

Central California bunchgrass prairies dominated by *N. pulchra* were first clearly described by Fremont (1848) in 1845 and Bryant (1985) in 1846, well before they were purportedly replaced by exotic annual grasses in the Central Valley. The bunchgrass prairies described by Fremont and Bryant were located, respectively, in the Sierra Nevada foothills and the inner Coast Ranges, however, and both authors clearly distinguished these upland prairies from quite different more continuous grasslands they found on the nearby Central Valley floor.

While traveling through the Sierra Nevada foothills in 1845, for example, Fremont reported that "Emerging from the woods, we rode about sixteen miles over an open prairie, partly covered with bunch grass, the timber reappearing on the rolling hills of the River Stanislaus in the usual belt of evergreen oaks." (Fremont 1848). A year earlier, in contrast, while camped at the site of the present city of Sacramento he found that "Here the grass is smooth and green, and the groves very open; the large oaks throwing a broad shade among sunny spots. . ." (McKelvey 1955). In my opinion Fremont's contrasting observations distinguish between *Leymus triticoides* prairie, which has a smooth aspect and numerous relict stands near Sacramento, and *Nasella*-dominated bunchgrass prairie, which has a rough aspect and many relict stands in the Sierra foothills.

Bryant similarly clearly distinguished central California prairies observed just four days and about 45 miles apart on an 1846 journey between what are now Sacramento and Alameda counties:

"September 14.—We crossed the Coscumne river [sic] about a mile from our camp, and travelled over a level plain covered with luxuriant grass and timbered with evergreen oak, until three o'clock, when we crossed the Mickelemes river [sic] . . . where . . . . The soil of the bottom appears to be very rich, and produces the finest qualities of grass.

"September 18.—. . . From this plain we entered a hilly country, covered to the summits of the elevations with wild oats and tufts or bunchs of a species of grass, which remains green through the whole season." (Bryant 1985).

It is clear Bryant on September 18 is describing his first observation of a *Nasella* species on hills near the present city of Livermore, where bunchgrass prairie relicts are still frequent. If the "luxuriant grass" he had seen four days earlier along the Cosumnes and Mokelumne rivers was also a bunchgrass, he would have said so. More likely it was *Leymus triticoides,* which still dominates numerous prairie relicts along those rivers and is the only common native or non-native Central Valley grass associated with oaks which would be "luxuriant" in September before irrigation was widely introduced to the Central Valley in the 1860's and 1870's (Hundley 1992).

Contrary to popular impression, the grassland vegetation of central California valley floors was clearly described well before 1850. Early accounts by travelers leave little doubt domination of valley grasslands by bunchgrasses like *N. pulchra* was generally absent in the period BDP assumes it occurred. Jedediah Smith, for example, camped twelve miles south of the American-Sacramento river confluence on February, 1828, and wrote: "The whole face of the country is a most beautiful green, resembling a flourishing wheat field". (Burcham 1957). The hummocky tussocks of bunchgrass prairies never produce smooth grass canopies characteristic of wheat fields, but relict native prairies near the site of Smith's camp (see below) still resemble wheat fields because of their domination by *L. triticoides,* a rhizomatous native perennial grass whose name reflects its strong resemblance to wheat.

Two years earlier, in 1826, Captain Beechey reported that three members of his expedition (Collie, Marsh, and Evans) described how a valley floor near what is now the border between San Mateo and Santa Clara counties "opened out on a wide country of meadow land, with clusters of fine oak free from underwood. It strongly resembled a nobleman's park" (McKelvey 1955). The European

parks familiar to members of this British expedition are dominated by stoloniferous or rhizomatous grasses like *Agrostis tenuis* Sibth. and *Poa pratensis* L. (Hessayon 1990; Jenkins 1994) resembling *L. triticoides* much more than non-rhizomatous *N. pulchra.* The site of this observation is now covered by highly urbanized "Silicon Valley", but relict native prairies dominated by *L. triticoides* are still present nearby at a sea level ecotone with saltmarsh located just across San Francisco Bay at Coyote Hills Regional Park (personal observation). Relict bunchgrass prairies dominated by *N. pulchra* do occur in hills east and west of the bay but are absent from plains near sea level.

A striking common feature of all these early accounts is the great similarity between what they reported and vegetation present in the same places today wherever landscapes have not been altered by agriculture or urbanization. That is not what the BDP predicts since it imagines California valleys were covered by *Nasella pulchra* before overgrazing in the 1850's and 1860's caused its replacement by exotic weedy species from Eurasia (Heady 1977). Traveler's reports from earlier periods make it clear, however, that two exotic Eurasian annuals, *Avena fatua* L. and *Erodium cicutarium* (L.) L'Hér., were common and dominant before 1850. Bryant's 1846 description, cited above, of wild oats and bunchgrass codominating a Coast Range hillside is a typical but not particularly early example of such reports (Bryant 1985). Oceanic pollen deposits of *E. cicutarium* in the Santa Barbara Basin demonstrate its abundance in the California Floristic Province by 1751–1765, well before California's first European settlement in 1769 and possibly the result of its introduction to the Baja Californian part of the province in the early 1750's by the Jesuit explorer Consag and subsequent explosive natural spread northward facilitated by openings created by pre-European burning. (Mensing and Byrne 1999). Its presence with *A. fatua* in adobe bricks of California's oldest European buildings (Burcham 1957) is consequently explained.

Vegetation surveys

Numerous small relict prairies are still extant in central California, where they are particularly frequent in Sacramento County near the places they were seen and described in the nineteenth century by Jedediah Smith, John C. Fremont, and Edwin Bryant. Most frequently these prairie remnants are dominated by *Leymus triticoides,* but two graminoid sedges, *Carex barbarae* Dewey and *C. praegracilis* W. Boott, are also often very important elements. Relict prairies near Sacramento occur both in the open and as groundcover in valley oak (*Quercus lobata* Nee) savannas, woodlands, and forests, which are all present at The Nature Conservancy's Cosumnes River Preserve in the southern part of the county. If "savanna" is interpreted

broadly enough to include open valley oak woodland, Griffin's (1977) statement "Relatively undisturbed savannas of *Quercus lobata* have not been available on prime alluvial soils for over a century . . ." fortunately does not accurately describe the Cosumnes Preserve.

A variety of plant communities occur at the reserve in a sequence which changes with increasing distance from its streams. Riparian forest dominated by *Populus fremontii* S. Watson occurs in the immediate vicinity of the Cosumnes River and its associated sloughs but is replaced by closed-canopy valley oak forest a short distance away from them. As distance from the river and sloughs increases, space between valley oak crowns also progressively enlarges so a vegetation sequence from closed forest through open woodland to savanna is formed. This sequence appears to result from a correlation between distance from rivers and sloughs and increasingly unfavorable soil conditions that may include greater competition for groundwater (Walter 1979) rather than from historic land uses since it is most evident where signs of disturbance are scarcest. In the sequence at the preserve from closed forest to savanna, valley oak density per hectare declines from 540 to 2.7 and soil shifts from Cosumnes silt loam to Dierssen sandy clay loam. The former is an Aquic Xerofluvent occurring on the Cosumnes River floodplain, and the latter, an Argic Durixeroll that is consequently much less permeable to both water and air, is on the rims of basins more distant from the river (Tugel 1991). The Cosumnes is one of California's few undammed rivers, and in most years large areas of the preserve are covered by winter flood waters, which often do not recede for several months.

At the preserve prairie vegetation is best developed as an understory in open valley oak forest. Cover estimates from twelve such stands are provided below (Table 1). All are on Cosumnes silt loam except 1 and 6, which respectively are on Dierssen sandy clay loam and Columbia sandy loam (Tugel 1991).

All the above stands were sampled between August and December, 1994, and are representative of open oak forest in the western and oldest part of the preserve. Some differences among them are evident, however. The lower valley oak cover of stand 3 indicates it is located at the open forest's outer edge ecotone with savanna, where soils become heavier and water stress greater. In contrast, significant *Vitis* and *Fraxinus* cover in stands 5–8 indicate their location is at open forest's inner edge ecotone with oak- and cottonwood- (*Populus*) dominated closed riparian forest, where soils are lighter and water stress reduced.

Similar open oak forest vegetation occurring on two recent additions to the preserve located east of its original oldest portion was sampled in May–June, 1995. The Orr Ranch addition, located immediately east of the original preserve, had been

TABLE 1. BRAUN-BLANQUET COVER-ABUNDANCE VALUES AND MEANS FOR SPECIES IN 12 OPEN OAK FOREST-RELICT PRAIRIE SAMPLE STANDS AT THE NATURE CONSERVANCY'S CONSUMNES RIVER PRESERVE. The cover class mean (with + assigned a value of 0.1) of each species is given at right.

Sample stand:	1	2	3	4	5	6	7	8	9	10	11	12	x̄
Quercus lobata	5	5	4	5	5	5	5	5	5	5	5	5	4.9
Leymus triticoides	4	3	1		5	5	5	2	2	4	2	1	2.8
Carex barbarae	3	4		1							5	5	1.5
Carex praegracilis	1		2	3				5	5	3	2	1	1.8
Rosa californica	1	1		1		1			1	+	1	1	0.6
Lolium multiflorum	2	3	5	4									1.3
Lactuca serriola	1	1	1	1							1		0.3
Toxicodendron diversilobum	+	+	2			1	2		1	+			0.5
Rumex crispus	2	1		1									0.3
Cichorium intybus	+	+	2	+				1	+	1	1	1	0.5
Convolvulus arvensis	+												0.0
Lotus corniculatus	1	1							+				0.2
Phyla nodiflora	1								1				0.2
Lotus purshianus	+												0.0
Lepidium latifolium	1												0.1
Carduus pycnocephalus		+											0.0
Atriplex triangularis		+											0.0
Raphanus sativus		+											0.0
Rumex conglomeratus		+					+	1	+	1	1		0.3
Cirsium vulgare		+		1						+	+		0.1
Picris echioides		+	1	1				+	1	1	+		0.4
Cordylanthus pilosus		2						+					0.2
Gylcyrrhiza lepidota		2											0.2
Lathyrus jepsonii		1											0.1
Asclepias fascicularis		1		+									0.1
Foeniculum vulgare		+											0.0
Plantago lanceolata		+		+									0.0
Plantago major								+					0.0
Barbarea vulgaris			1					+					0.1
Cyperus eragrostis			+					1	1				0.2
Fraxinus latifolia			1	2	2	2	2	1	2	1	2	2	1.3
Epilobium brachycarpum			+										0.0
Vitis californica					2	1	3	1					0.6
Aster chilensis								+					0.0
Mentha pulegium								+					0.0
Euthamia occidentalis					1		1					1	0.3
Rubus ursinus					2		2	+	1	+			0.4
Acer negundo												2	0.3
Cornus glabrata													0.2
Rubus discolor							1		1	1			0.3
Xanthium strumarium							2				+		0.0
Salix exigua						2						1	0.1
Asparagus officinalis		+			+			1	1	1			0.3
Rumex pulcher		1	+										0.1

acquired a short time before the survey, while the Valensin Ranch, located somewhat farther east near Highway 99, was acquired by the preserve after the survey. The superior floristic richness of the addition surveys (Table 2) reflects their spring-summer (rather than summer-fall) timing and the outstanding condition of open oak forest at Valensin Ranch. The Orr Ranch sample is on Dierssen sandy clay loam and the Valensin on Liveoak sandy clay loam (Tugel 1991).

Not all vegetation at the Cosumnes Preserve is open oak forest. Three stands representative, respectively, of open savanna (OS), oak-dominated closed riparian forest (OR), and cottonwood-dom-

inated closed riparian forest (CR) sampled in September, 1994, are provided below in Table 3. The open savanna sample stand is on Dierssen sandy clay loam, and the two riparian forest sample stands are on Columbia sandy loam (Tugel 1991).

The great difference between savanna and closed riparian forest vegetation is evident in Table 3 since valley oak is their sole species in common. The oak and cottonwood dominated types of closed riparian forest are much more similar, however, and have many species in common since both are subject to frequent extended flooding. Such flooding also prevents development of a graminoid understory, and its absence readily distinguishes them from open

TABLE 2. BRAUN-BLANQUET COVER-ABUNDANCE VALUES AND MEANS FOR SPECIES IN 2 OPEN OAK FOREST-RELICT PRAIRIE SAMPLE STANDS LOCATED, RESPECTIVELY, AT ORR AND VALENSIN RANCHES IN THE NATURE CONSERVANCY'S COSUMNES RIVER PRESERVE.

Sample stand:	Orr Ranch	Valensin Ranch	x̄
Quercus lobata	5	5	5.0
Leymus triticoides	2	2	2.0
Anthemis cotula	2	+	1.1
Cichorium intybus	2		1.0
Lolium multiflorum	2	1	1.5
Bidens frondosa	1	+	0.6
Stellaria media	2	+	1.1
Vicia sativa	1		0.5
Conium maculatum	1	+	0.6
Lythrum hyssopifolium	1	1	1.0
Carex praegracilis	2	1	1.5
Carex barbarae	2	4	3.0
Cyperus eragrostis	+	1	0.6
Lactuca serriola	+	+	0.1
Rumex conglomeratus	1	1	1.0
Raphanus sativus	+	+	0.1
Rumex crispus	1	1	1.0
Toxicodendron diversilobum	1	+	0.6
Sisymbrium officinale	1	+	0.6
Solanum americanum	1	+	0.6
Chenopodium ambrosioides	1		0.5
Sonchus oleraceus	+		0.1
Hordeum murinum	+	+	0.1
Bromus diandrus	+	+	0.1
Cirsium vulgare	+		0.1
Melilotus indica	+		0.1
Chlorogalum pomeridianum	1	1	1.0
Polygonum punctatum		2	1.0
Rumex pulcher		1	0.5
Rubus discolor		+	0.1
Xanthium strumarium		1	0.5
Ranunculus muricatus		+	0.1
Sonchus asper		+	0.1
Geranium dissectum		+	0.1
Rosa californica		+	0.1
Atriplex triangularis		+	0.1
Phyla nodiflora		1	0.5
Convolvulus arvensis		+	0.1
Stachys ajugoides		+	0.1
Brodiaea elegans		+	0.1
Ammi visnaga		+	0.1
Amaranthus albus		+	0.1
Anthriscus caucalis		+	0.1
Polypogon monspeliensis		+	0.1
Dipsacus fullonum		+	0.1
Maclura pomifera		+	0.1
Mimulus gutatus		+	0.1
Medicago arabica		+	0.1
Plantago major		+	0.1
Juncus xiphioides		+	0.1

TABLE 3. BRAUN-BLANQUET COVER-ABUNDANCE VALUES FOR SPECIES IN REPRESENTATIVE OPEN SAVANNA (OS), OAK-DOMINATED CLOSED RIPARIAN FOREST (OR), AND COTTONWOOD-DOMINATED CLOSED RIPARIAN FOREST (CR) SAMPLE STANDS AT THE CONSERVANCY'S COSUMNES RIVER PRESERVE.

Sample stand:	OS	OR	CR
Quercus lobata	2	5	3
Lolium multiflorum	5		
Distichlis spicata	2		
Lactuca serriola	2		
Rumex crispus	1		
Hirschfeldia incana	2		
Centaurea solstitialis	1		
Bromus hordeaceus	2		
Hordeum marinum	2		
Leymus triticoides	2		
Grindelia camporum	1		
Rumex pulcher	+		
Rubus ursinus		5	1
Vitis californica		3	+
Acer negundo		2	
Cyperus eragrostis		2	2
Rosa californica		1	1
Rubus discolor		1	3
Fraxinus latifolia		1	3
Cirsium vulgare		1	
Picris echioides		1	1
Rumex conglomeratus		+	+
Populus fremontii			5
Euthamia occidentalis			2
Plantago major			1
Oenanthe sarmentosa			+
Cephalanthus occidentalis			2
Polygonum punctatum			1
Artemisia douglasiana			+
Urtica dioica			+

The lower cover of the native prairie grass *Leymus triticoides* in open savanna relative to open oak forest at the Cosumnes Preserve appears to contradict the early reports discussed above that suggest it once dominated many of California's open areas. Evidence of prairie remnants in open areas farther north in Sacramento County at the new Stone Lakes National Wildlife Refuge supports the reports, however, and suggests present scarcity of native prairie grass in the Cosumnes savannas results from former cultivation, which did not occur in the open forests. The preserve is now planting trees to restore extensive areas where they were removed to facilitate farming, but cultivation often occurred in the savannas without general removal of their widely scattered large valley oaks.

In June–July, 1995, two prairie remnants were located at Stone Lakes refuge in open grassland lacking valley oaks or other woody plants and subsequently sampled. The larger, which covered 930 m² and is on Dierssen sandy clay loam, is represented in Table 4 below by sample SL1, while the smaller, SL2, covered 56 m² and is on Clear Lake clay (Tugel 1991). Three contemporary samples

oak forest. Most species largely confined to the cottonwood-dominated phase of closed riparian forest, including *Populus fremontii* itself and *Cephalanthus occidentalis* L., are particularly adapted to very frequent flooding and associated coarse alluvial soils (Holstein 1984).

TABLE 4. BRAUN-BLANQUET COVER-ABUNDANCE VALUES FOR SPECIES AT FIVE SACRAMENTO COUNTY SAMPLE STANDS. Three (MC 1–3) are in oak forest along Morrison Creek and two (SL 1–2) are in relict prairies at Stone Lakes National Wildlife Refuge.

Sample stand:	MC1	MC2	MC3	SL1	SL2
Quercus lobata	5	5	5		
Leymus triticoides	1	4	5	5	5
Rubus ursinus	5		2		
Sambucus mexicanus	1		1		
Toxicodendron diversilobum	2	1	2		
Foeniculum vulgare	+		1		
Juglans hindsii	+	+			
Rubus discolor	1		1		
Cornus glabrata	1				
Rosa californica	1				
Vitis californica	+		+		
Prunus cerasifera	+		1		
Lactuca serriola		2			
Bromus diandrus		2	+	2	
Lolium multiforum		2	+		
Stellaria media		3	+		
Sisymbrium officinale		2			
Sonchus oleraceus		1	1		
Rumex conglomeratus		1	+		
Raphanus sativus		1	1	+	
Convolvulus arvensis		1	+	+	1
Rumex crispus		1	+		1
Bidens frondosa		1	+		
Urtica urens		+			
Chenopodium berlandieri		1	+		+
Atriplex triangularis		+	+		
Chenopodium murale		+			
Xanthium strumarium		+	1		2
Asparagus officinalis		+	1		
Galium aparine		+			
Solanum americanum			+		
Lepidium latifolium			+		
Malva nicaeensis			+		
Cyperus eragrostis			+		
Avena fatua				2	
Vicia villosa				2	
Trifolium hirtum				+	
Hemizonia pungens					1
Rorippa palustris					+
Hirschfeldia incana					1
Helianthus annuus					+
Phyla nodiflora					1
Gnaphalium luteo-album					+
Anthemis cotula					+
Polygonum arenastrum					1

from oak forest along Morrison Creek a short distance north of the refuge are provided for comparison. These resemble similar forest at the Cosumnes Preserve, and consist of one oak-dominated closed riparian forest sample, MC1, and two open oak forest samples, MC2 and MC3. All are on Egbert clay (Tugel 1991).

In July–August, 1995, five additional native prairie remnants varying in area from 230 to 470 m² and resembling the Stone Lakes remnants in having few woody plants were located and sampled on Coast Range hillslopes in northwestern Contra Costa County. They are represented below by samples

CC 1–5 in Table 5. CC 1 and 2 are on Sehorn clay, CC 3 and 4 are on Millsholm loam, and CC 5 is on Clear Lake clay (Welch 1977).

DISCUSSION

Several theoreticians important in the first half of the twentieth century like J.C. Willis, Sigmund Freud, and Frederic Clements later fell from favor when it became clear their theories did not describe reality. That happened for Clements in at least two areas. He was a leading American opponent of Darwinian evolution (Hagen 1992), the central para-

TABLE 5. BRAUN-BLANQUET COVER-ABUNDANCE VALUES AND MEANS FOR SPECIES AT 5 RELICT PRAIRIE SAMPLE STANDS ON COAST RANGE HILLSLOPES IN NORTHWESTERN CONTRA COSTA COUNTY.

Sample stand:	CC1	CC2	CC3	CC4	CC5	x̄
Leymus triticoides	3	4	5	5	5	4.4
Silybum marianum	1				+	0.2
Carduus pycnocephalus	1	1	2	2	2	1.6
Sonchus oleraceus	1					0.2
Lactuca serriola	1	1	1	1	1	1.0
Avena fatua	2	1			1	0.8
Brassica nigra	4					0.8
Toxicodendron diversilobum		2				0.4
Aira caryophyllea		3	2	2		1.4
Vulpia myuros		2	2	2		1.2
Conium maculatum			1			0.2
Epilobium brachycarpum			1	1		0.4
Picris echioides			1		1	0.4
Brassica rapa			1		1	0.4
Chlorogalum pomeridianum			1			0.2
Hirschfeldia incana			1			0.2
Clarkia unguiculata			2	1		0.6
Madia gracilis			2			0.4
Phleum pratense			2			0.4
Sonchus asper			1			0.2
Bromus madritensis			1			0.2
Scrophularia californica				+		0.0
Amsinckia menziesii				1		0.2
Gnaphalium californicum				1		0.2
Geranium dissectum					1	0.2
Bromus diandrus					1	0.2

digm of biology, and developed monoclimax theory, which assumed vegetation in each climate zone converges toward a common type (Hamilton 1997). Monoclimax was long influential but has gradually failed as evidence accumulated that climate is one of the least stable environmental factors. In California, for example, the climate 150 years ago in the Little Ice Age was significantly colder and wetter than at present during the lifetimes of many individual trees in old growth forests (Bradley 1999; Fagan 2000).

Theories inaccurately describing reality are clearly social constructions even when arising within science, but recently some elements in the humanities have claimed all science and even reality itself is a social construct (Gross and Levitt 1994; Sokal and Bricmont 1998). Such claims may just be new weapons in an old war for academic influence, but science still needs to police itself and eliminate any lingering social constructs it still contains. The BDP appears to be a good example, but Clements should not entirely be blamed for that. He eventually recognized *Leymus triticoides* formerly dominated much of the Central Valley (Clements and Shelford 1939), but by that time his academic influence had waned (Hagen 1992) and the world was more preoccupied by war than science. It was later figures like Heady (1977) who provided the dogmatic character of today's BDP. Before then opinion regarding California grassland ecology was more eclectic. The conclusions of Biswell (1956) and

Burcham (1957), for example, are generally compatible with my field observations; those of Heady are not.

So what were California's pre-agricultural grasslands really like? The vegetation samples reported above and numerous other field observations suggest sufficient relict evidence remains to reasonably reconstruct their basic nature. *Leymus triticoides* dominated most central California grasslands on sites with clay or loam soil, flat to moderately sloping topography, precipitation above 250 mm per year, and moderate to high fertility. Relict stands of *L. triticoides* are frequent on such sites, but more often they are dominated by *Lolium multiflorum* Lam., *Bromus diandrus* Roth, or *Avena fatua*. Similarly frequent relict stands of *Nassella pulchra* suggest pre-agricultural dominance shifted to it on sites with steeper slopes, coarser soils, and lower fertility; which today are most frequently dominated by *Bromus hordeaceus* L., *Avena barbata* Link, *Cynosurus echinatus* L., and *Taeniatherum caput-medusae* (L.) Nevski. Wester (1981) previously argued that arid valleys like the southern San Joaquin with precipitation <250 mm per year were pre-agriculturally dominated by annual rather than perennial species. Such annuals were largely spring-active forbs.

Three interesting questions remain:

1. Is *L. triticoides* always *L. triticoides*?
Stebbins and Walters (1949) concluded from

their chromosome and hybridization studies of *L. triticoides* and *L. condensatus* (C. Presl) A. Löve that much of the grass traditionally called *L. triticoides* in central California is actually a largely sterile hybrid between that species and *L. condensatus.* They strongly implied the hybrid, which they called *Elymus triticoides* Buckl. ssp. *multiflorus* Gould and distinguished from typical *L. triticoides* by its possession of 3 to 7 rather than 2 spikelets per central spike node, is much more common than either of its parents and includes all hillslope populations like those from northwestern Contra Costa County sampled above. I don't doubt their conclusions since the senior author's contributions to California plant evolution remain unequaled and partial sterility arising from natural hybridization accounts for the rarity of viable seed in the central California grass currently most often called *L. triticoides.* Nevertheless, the current name for *E. triticoides* ssp. *multiflorus* is *L.* ×*multiflorus* (Gould) Barkworth, a grass far too large (Barkworth 1993) to match Stebbins and Walters' abundant hybrid or any of the *Leymus* populations sampled above. Recent central California local floras (Best et al. 1996; Ertter 1997; Matthews 1997; Oswald and Ahart 1994) also fail to follow Stebbins and Walters' taxonomy since all treat *L. triticoides* as common and *L.* ×*multiflorus* as rare to completely absent. Hybrid or not, the common central California *Leymus,* because of its small size and strongly rhizomatous habit, is physiognomically close to typical *L. triticoides* and distant from *L. condensatus,* which is only weakly rhizomatous and one of California's largest native upland grasses. All stands sampled above matched *L. tritcoides* in size and were strongly rhizomatous; so much so that stands and single clones were probably often equivalent. Consequently the name *L. triticoides* is applied here to all samples even though, following Stebbins and Walters (1949), it is likely their fertility is depressed through introgression from the *L. condensatus* genome.

2. If the BDP is wrong, why is *Nassella pulchra* at Jepson Prairie?

Nassella pulchra is common on the Central Valley floor in at least one place, the Jepson Prairie Preserve located in Solano County at the northern edge of the Montezuma Hills. Since the preserve has generally flat topography, the above discussion might lead to the expectation it is dominated by *Leymus triticoides,* which is actually rare to absent there. How is that accounted for? One explanation, of course, is that the BDP is true despite arguments against it provided here. Wester (1981) provided another when he concluded "Areas of bunchgrass [at Jepson Prairie] occupy relatively moist sites influenced by the cool, humid, maritime air able to penetrate to this part of the Central Valley through the San Francisco Bay gap. These conditions are not typical over the remainder of the Valley." His

conclusion has merit since the distribution of *Nassella pulchra* in California closely matches oak woodland (Beetle 1947; Dremann 1987), and several species associated with that vegetation type occur on the Central Valley only where the flow of maritime air is strongest. Examples are the occurrence of the trees *Quercus agrifolia* Nee and *Aesculus californica* (Spach) Nutt. (Griffin and Critchfield 1972; personal observation) and the mammals *Sylvilagus bachmani riparius* (riparian brush rabbit) and *Neotoma fuscipes riparia* (riparian woodrat) (Zeiner et al. 1990) in a localized area of the Central Valley floor that includes San Joaquin and southern Sacramento counties. What Wester's hypothesis does not explain is why *L. triticoides* rather than *N. pulchra* is dominant in northwestern Contra Costa County, where flow of maritime air is even stronger than at Jepson Prairie.

As discussed above, *L. triticoides* is favored by heavy clay and loam soils and *N. pulchra* by lighter ones since bunchgrasses are better adapted for drought stress than rhizomatous grasses (Grime 1979). The clay favored by *L. triticoides* holds more water than the light, frequently sandy soils hosting *N. pulchra* (Kramer 1969), and the latter's usual occurrence on slopes also accelerates runoff and consequent drought stress. In northwestern Contra Costa County, for example, *L. triticoides* occurs on a series of relatively heavy soils: Clear Lake, Diablo, and Sehorn clays; Conejo, Lodo, and Los Osos clay loams; and Los Gatos, Millsholm, and Tierra loams (Welch 1977). At Jepson Prairie, in contrast, *N. pulchra* occurs on a light soil, San Ysidro sandy loam (Bates 1977); an environmental factor accounting for the vegetational difference between the two relict prairie areas better than maritime air flow. Light soils may also account for Clements' momentous observation of *N. pulchra* near Fresno since a large area of sandy soil derived from Kings Canyon's glacial outwash occurs near there (Storie and Weir 1951). Even on generally flat valley floors aeolian movement of sand creates hummocky microtopography (Selby 1985) containing small versions of the slopes favored by *N. pulchra.* Grassland on sandy soil is among California's least known vegetation types since its ease of cultivation made it particularly attractive to early valley farmers. Consequently a high percentage of California's extinct plant species (e.g., *Eriogonum truncatum* Torrey and A. Gray and *Monardella leucocephala* A. Gray) were associated with sandy grassland (Skinner and Pavlik 1994). *N. pulchra* at Jepson Prairie now faces a different threat, overprotection. It has steadily declined there since preserve establishment eliminated even the light grazing required to maintain grass diversity by causing release from exotic annual competition (Howe 1999). Ironically grazing elimination at Jepson Prairie was motivated by BDP myths.

TABLE 6. BRAUN-BLANQUET COVER-ABUNDANCE VALUES FOR SEVERAL RELICT PRAIRIE SAMPLE STANDS: FIVE (WITH MEANS) NEAR FOLSOM IN SACRAMENTO COUNTY (F 1–5), ONE NEAR GREEN ISLAND IN NAPA COUNTY (N1), AND ONE NORTH OF FAIRFIELD IN SOLANO COUNTY (L).

Sample stand:	F1	F2	F3	F4	F5	$\bar{x}$ (of F)	N1	L
Holocarpha virgata	4	4	4	4	4	4.0		
Taeniatherum caput-medusae	3	3	3	3	3	3.0	1	
Bromus hordeaceus	2		1	1	1	1.0	1	2
Leontodon taraxacoides	2	1	2	2	2	1.8		
Lolium multiflorum	1	1	2	1	1	1.2	5	
Briza minor	2	2	2	2	2	2.0	+	
Trifolium microcephalum		+				0.0		
Castilleja attenuata		+			+	0.0		
Hemizonia congesta							4	
Centaurea calcitrapa							2	
Vulpia myuros							1	
Xanthium strumarium							1	
Picris echioides							1	
Polypogon monspeliensis							1	
Rumex crispus							1	
Rumex pulcher							1	
Convolvulus arvensis							1	
Cichorium intybus							1	
Centaurea solstitialis							1	5
Cirsium vulgare							1	
Lythrum hyssopifolium							1	
Hypochaeris radicata							1	
Hordeum marinum							1	1
Bellardia trixago							1	
Kickxia elatine							1	
Eremocarpus setigerus							1	
Polygonum arenastrum							+	
Raphanus sativus							+	
Agrostis avenacea							+	
Plantago lanceolata							+	
Epilobium brachycarpum							+	
Sonchus oleraceus							+	
Juncus bufonius							+	
Malvella leprosa							+	
Lactuca saligna							+	
Crypsis schoenoides							+	
Lactuca serriola							+	
Bromus diandrus							+	1
Lepidium latifolium							+	
Foeniculum vulgare							+	
Phalaris aquatica							+	
Eryngium aristulatum							+	
Hirschfeldia incana							+	
Leymus triticoides							+	
Distichlis spicata							+	
Amaranthus hybridus							+	
Avena barbata							+	
Hordeum murinum							+	1
Hemizonia corymbosa							+	
Malva nicaeensis							+	
Cynodon dactylon							+	
Ammi majus							+	
Erodium cicutarium							+	
Atriplex triangularis							+	
Carduus pycnocephalus							+	
Hordeum brachyantherum							+	
Lupinus formosus								2

3. What was on the old terraces?

A significant area of California mapped as bunchgrass prairie in accordance with the BDP (Kuchler 1964) has precipitation too high to fit Wester's ephemeral annual model (Wester 1981) and lacks both modal environmental conditions and relict examples of *L. triticoides* and *N. pulchra.* Along the eastern edge of the Central Valley a nearly continuous band of old terraces (Wahrhaftig and Birman 1965) is characterized by flat topography and infertile duripan soils like Redding loam (Tugel 1991). Old terraces have received attention because most California vernal pools occur there, but uplands around the pools are largely ignored. As in other California lowlands, exotic annual grasses like *B. hordeaceus, T. caput-medusae,* and *Aegilops triuncialis* L. are important elements of current old terrace vegetation, but it is also frequently dominated by a native plant remaining photosynthetically active throughout long, dry Central Valley summers. BMD predicts this old terrace dominant will be a bunchgrass, but it isn't. It isn't even a grass. The native dominating many square miles of California's old terraces is, *Holocarpha virgata* (A. Gray) Keck, and other tarweeds like *Hemizonia congesta* DC. dominate extensive areas regularly mapped as grassland elsewhere in California. Despite their dominance of much California vegetation, however, the first of these tarweeds is not mentioned in two of the most extensive recent treatments of state vegetation (Barbour and Major 1977; Sawyer and Keeler-Wolf 1995), and the second appears just once (as *Hemizonia multicaulis* H. & A., a synonym) without comment in one of the former's tables. There is little doubt these vegetationally important native tarweeds were ignored because of the BDP. They went unnoticed because they aren't bunchgrasses or even grasses despite their extensive dominance of "grassland". At this time It can't be proved conclusively these native tarweeds were as dominant pre-agriculturally as they are now, but the burden of proof they weren't rests on advocates of the BDP.

The dominant tarweeds resemble low-precipitation area dominants in being annual forbs but differ in being more productive in summer than spring because they can tap summer soil water unavailable to most other plant species (Walter 1979). *Centaurea solstitialis* L., an exotic weed, uses a similar adaptive strategy to destructively invade rangeland throughout northern California (Thomsen et al. 1996).

In valley and foothill prairie remnants with soils similar to those most suitable for bunchgrasses another forb, *Lupinus formosus* E. Greene, is frequent that differs from tarweeds in being perennial. It occurs at Stone Lakes refuge away from *Leymus triticoides* on somewhat sandier sites, is frequent on Delhi sands in Merced County, and also occurs on steep Coast Range foothills north of Fairfield in Solano County.

Table 6 presents five July, 1999, sample stands of tarweed-dominated vegetation on Argonaut-Auburn complex soils (Tugel 1991) along East Bidwell Road near Folsom, Sacramento County (F 1–5); a single September, 1998, sample stand on Haire loam (Lambert and Kashiwagi 1978) near Green Island Road in Napa County (N1); and a single August, 1999, lupine prairie sample stand on Dibble-Los Osos loams (Batel 1977) north of Fairfield in Solano County (L). The greater diversity of the Napa County sample is only partially real since it covered a larger and less homogeneous area.

CONCLUSIONS

Clements should not be blamed for the BDP's current dogmatism. His observations in California were limited, and his last publication dealing with its grasslands (Clements and Shelford 1939) before his 1945 death is reasonably accurate. The BDP hardened into dogma only later. Criticism of Clements and the BPD does not mean the end of knowledge about pre-agricultural California grasslands or resurrection of bizarre theories that they were once covered by chaparral (Hamilton 1997, Cooper 1922). Early descriptions and current relict vegetation provide a congruent picture of diverse grassland vegetation in pre-agricultural California reflecting similar diversity of climate, geology, and soils. Some important elements are becoming known. It is time to identify the rest in an atmosphere free from dogma.

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THE POLLINATION BIOLOGY OF *ERIASTRUM DENSIFOLIUM* SSP. *SANCTORUM* (POLEMONIACEAE), AN ENDANGERED PLANT

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Abstract

An analysis of the reproductive biology of the Santa Ana Woolly Star, *Eriastrum densifolium* ssp. *sanctorum* (Milliken) H. Mason shows that the primary pollinators of this rare and endangered plant include the Giant Flower-loving Fly, hummingbirds, bumble bees, halictid bees, and digger bees. In comparison to previous studies (Munoz 1991; Erickson 1993; Stone 1995), fewer individuals of each pollinating species were present in this study suggesting that overall fruit set may be declining. However, seed set per fruit appears to be similar to values found in earlier studies indicating that pollinator efficiency is not a limiting factor. In fact, the three principal pollinators that were tested were all reasonably efficient pollen vectors. Only a single simulated pollination event was usually required to effect normal fruit and seed set, indicating that this plant is not dependent on any single pollinator for its reproductive success. The flowers produced an average of nearly 2 μl of nectar per flower, which is in the range of insect pollinated plants.

Eriastrum densifolium ssp. *sanctorum* (Milliken) Mason (Polemoniaceae), the Santa Ana River Woolly Star, (*Eds*), is one of the 12 most endangered plants in California (York 1987). Research toward understanding and preserving this plant has been conducted for more than a decade by faculty and students at California State University, Fullerton (CSUF). *Eds* is distinguished from the other subspecies by the presence of a very long floral tube that normally exceeds 25 mm in length (Brunell, 1999). This short-lived, perennial subshrub with woolly pubescence occupies sand terraces within the floodplain of the Santa Ana River at the base of the San Bernardino Mountains in San Bernardino County, California (Munoz 1991, Brunell 1996, 1999). The restricted distribution of *Eds* and loss of habitat led to the listing of the subspecies as endangered by the United States Fish and Wildlife Service (USFWS) in 1987. The completed Seven Oaks Dam is expected to further imperil the survival of this species by reducing the deposition of new sand that is required for the establishment of new populations (Burk et al. 1988). A management plan for the Santa Ana River Woolly Star (Burk and Jones 1993) was approved in November of 1993 with the goal of maintaining a healthy and genetically viable *Eds* population.

A detailed knowledge of the pollination biology of any species is valuable, but this knowledge often becomes critical when trying to prevent rare and endangered species from becoming extinct. It is of little use to preserve habitat for an endangered plant species if, at the same time, the habitat for its pollen

vectors is destroyed. The intent of these studies was to augment the existing knowledge of *Eds* presented elsewhere (see Zembal and Kramer 1985; Burk et al. 1988; Burk et al. 1989; Munoz 1991; Burk and Jones 1993; Erickson 1993; Stone 1995; Jones and Burk 1996). In addition to pollination biology, studies were conducted on the breeding biology of *Eds* (in prep.) and the life history of two of its principle pollinators, *Rhaphiomidas acton* (Steinberg et al. 1998) and *Halictus tripartitus* (in preparation). Although other studies were completed on the pollination biology of this species, this is the first study in which the research was conducted simultaneously over the entire extant range of *Eds* in the Santa Ana River Wash north of Redlands, California, in the country of San Bernardino.

Methods

Study areas. Five study sites, located within the Santa Ana River floodplain north of Redlands, San Bernardino County, California, were selected to cover the range of habitats and habitat ages within the floodplain that currently support all known populations of *Eds* (see Fig. 1). Three plots, where 100 or more *Eds* individuals formed a continuous population, were established in the immediate vicinity of each of the 5 study sites for a total of 15 study plots. All work presented here was completed within these plots.

Diurnal observation. To determine the major pollinators of *Eds* at each of the 5 Study Sites, a series of 9 "dawn to dusk" observations were conducted between 19 June and 6 July 1995. At each of the 5 study sites, three sets of three-day sequences of dawn to dusk observations were conducted for a total of 15-day sequences. The first sequence was done during the early blooming period, June 19 to

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[1] This paper is dedicated to the memory of Deborah K. Dorsett, who died 29 April 1999 in a tragic automobile accident. Deborah was an outstanding biologist, writer, and human being.
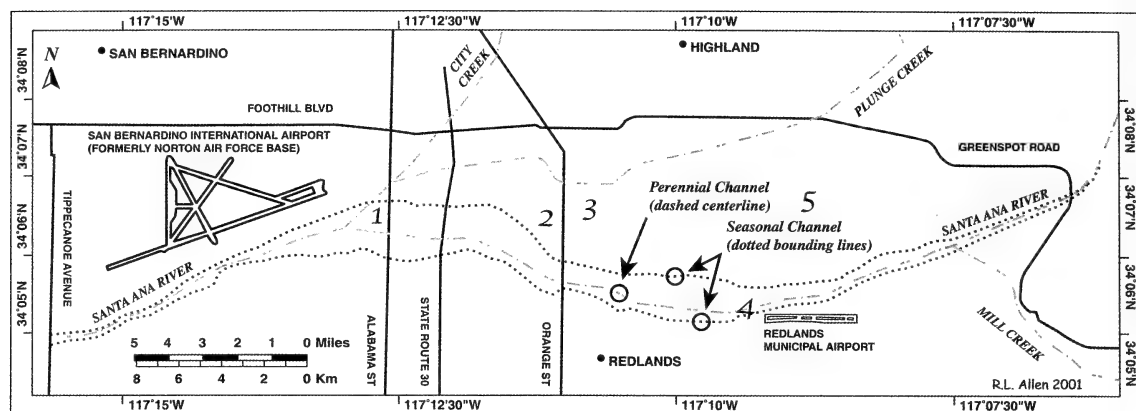
Fig. 1. Range and study locations for *Eriastrum densifolium* ssp. *sanctorum*. Dashed lines indicate tributary creeks and the perennial channel of the Santa Ana River. Dotted lines indicate the seasonal channel of the river. Gray shading shows the entire known modern range of *Eds*. The numbers 1, 2, 3, 4, and 5 indicate study locations.

22 1995, when approximately 25% of the *Eds* plants in a given study plot were in bloom. The second sequence was completed during the mid blooming period, June 26–28 1995, when about 50% of the *Eds* plants in a given study plot were in bloom. The final sequence was done during the late blooming period, July 3–6 1995, when approximately 75% of the plants had finished blooming.

Observations were conducted for 12 daylight hours beginning at 0700 and continuing until 1900 hours on each of the study days. At each study site, observations of approximately 15–20 *Eds* plants at plot number 1 started on the hour and continued until 10 minutes after the hour. Next the observer would move to plot number 2 within the same study site and observe approximately 15–20 *Eds* plants from 20 minutes after the hour until 30 minutes after the hour. Finally the observer would move on to plot number 3, the last plot in each study site, where 15–20 *Eds* plants were observed from 40 minutes after the hour until 50 minutes after the hour. This observation sequence continued hourly throughout the day from 0700 until 1900.

Observations were completed simultaneously at all 5 of the study areas by 5 different observers. Therefore, in each 12 hour observation period, 6 hours of pollinator observations were recorded for each site or a total of 30 hours of observation of pollinator activity on *Eds* plants each day throughout the distribution of this subspecies. All flower visitors that made contact with the anthers, the stigma branches, or both were recorded. Insect visitors were identified using a reference collection developed by Douglas Stone during his work on *Eds* (Stone 1995). All insects were identified and/or verified by Roy Snelling of the Natural History Museum of Los Angeles County.

Nectar rewards. Average nectar volume produced per flower was determined by using Drummond "Microcaps" microcapillary tubes. Five flowers on each of 10 plants in each of the 3 plots at each of the 5 study sites were sampled between 20 June and 26 June 1995 for a total of 750 flowers sampled. The flowers sampled were bagged prior to anthesis and nectar was sampled and measured during the morning hours once the flower buds had fully opened (usually within two days of bagging the buds).

Pollinator constancy. Tests to determine pollinator constancy were conducted by collecting pollen-laden specimens of each of the primary *Eds* insect pollinators (see Table 2 for the species sampled). All insects used to determine pollinator constancy were collected between 3 July and 6 July 1995 and between 7 June and 18 June 1996 as they visited *Eds*. The insects were killed and brought back to the laboratory where the purity of their pollen loads was determined. All insects were pinned for identification. No hummingbirds were sampled.

Pollen samples were carefully removed from each of the pollinators collected. Pollen was then placed on a microscope slide, covered by a drop of glycerol, and then covered by a glass cover slip. The slides were examined using a compound microscope, and the number and frequency of each different type of pollen was determined. For each pollen load, the number of *Eds* pollen grains and the number of non-*Eds* pollen grains were counted. The percent constancy was determined by dividing the number of *Eds* pollen grains by the total number of pollen grains of all types counted. The number of different pollen types present provides an estimate of the different flowering plant species each flower visitor to *Eds* is visiting. Thus, percent constancy data can be used as an estimate of the relative constancy of a given pollinator to *Eds*. For the purpose of this paper, a pollinator will be considered to be a "constant" pollinator for a particular species when that pollinator visits only that plant species during a single foraging flight.
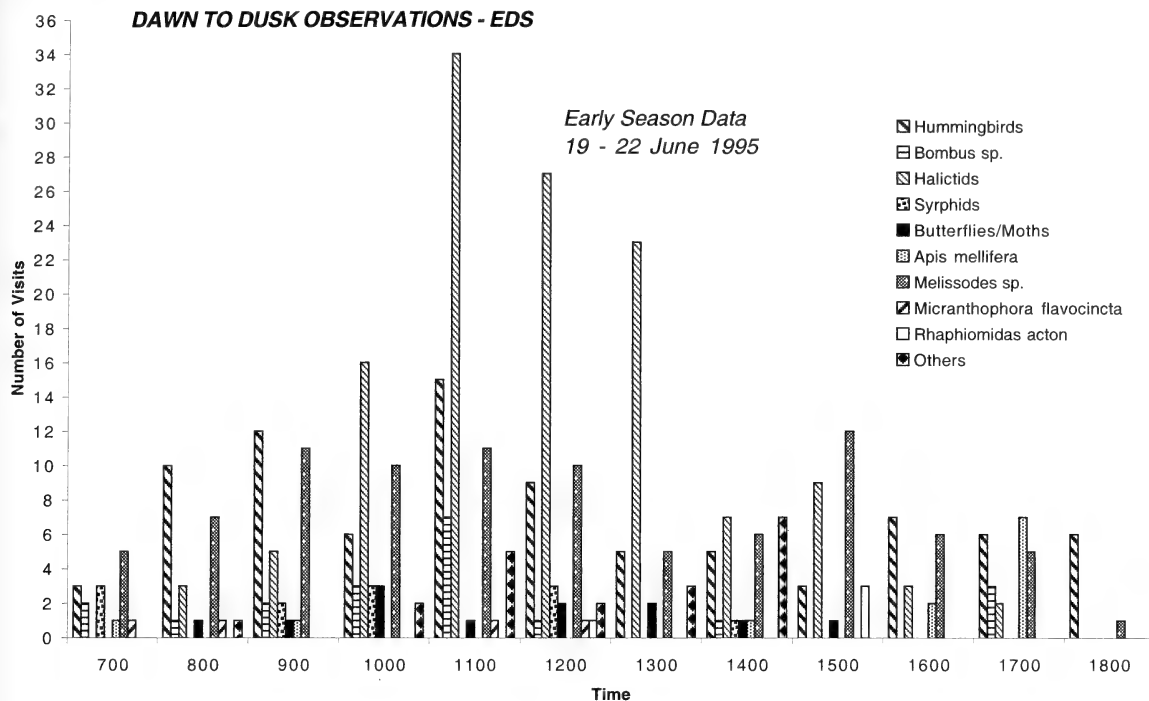
FIG. 2. Observations of pollinators on literally hundreds of flowers on 45–60 large plants of Eds—270 hours of observations were recorded during this period.

Pollinator efficiency. Pollinator efficiency is a measure of how effective a given flower visitor is at pollinating a given plant. Using the data from the "dawn to dusk" observations, we determined that the three most important pollination vectors visiting *Eds* during the 1996 flowering season were bumblebees, (*Bombus* spp.), hummingbirds and the Giant Flower-loving Fly, (*Rhaphiomidas acton* (see Steinberg, et al. 1998, for a discussion on the subspecific designation of this fly). We determined how each of these principal pollinators effects pollination by carefully observing which portions of the pollinators bodies came into contact with the anthers and stigmas in each flower.

Six inflorescences on each of 5 plants at each of the 5 Study Sites were emasculated in the bud stage and covered with a pollinator exclusion bag. Pollinator exclusion bags were obtained by purchasing brown (suntan) nylon anklet stockings and cutting approximately 20 cm lengths including the toe portion. The nylon bags were placed over an *Eds* inflorescence and secured with a twist tie. The flowers were marked by placing a drop of Elmer's fluorescent glue on a sepal of the flower bud to be used. Approximately two days after bagging was completed, and when three flowers on each of the 5 plants at each of the 5 study sites had opened and were ready to be pollinated, freshly killed specimens of *Bombus californicus* and *Rhaphidiomidas acton* and the head of a stuffed Anna's hummingbird from the teaching collection at CSUF, were in-

serted into an open flower of a nearby plant in a manner that mimicked, as closely as possible, the way a living individual approaches a flower. This procedure resulted in pollen deposition in the normal location for each of the principal pollination vectors. Each individual was then inserted into one of the bagged and emasculated test flowers. This procedure was repeated for each of the 3 principal pollination vectors until all the emasculated test flowers had received a single "visit" by each principal pollinator.

To determine the possible effect of repeated pollinator visits, the entire procedure was repeated with a second set of flowers, but instead of a single insertion, each pollinator was inserted twice into each emasculated test flower. The fruit and seed set per the number of flowers pollinated in all procedures was determined and provides an estimate of the relative pollinator efficiency for the three principal pollinators of *Eds* in 1996. In addition, three fruits were collected from each of the study plants. These fruits were used as controls to determine the average seed set per pollinated flower in open-pollinated, non-manipulated situations.

RESULTS

Diurnal observations. The dawn to dusk pollinator observations are presented in Figs. 2, 3, and 4. All plots in all 5 Study Sites were summed and are presented for the early season (Fig. 2), mid sea-
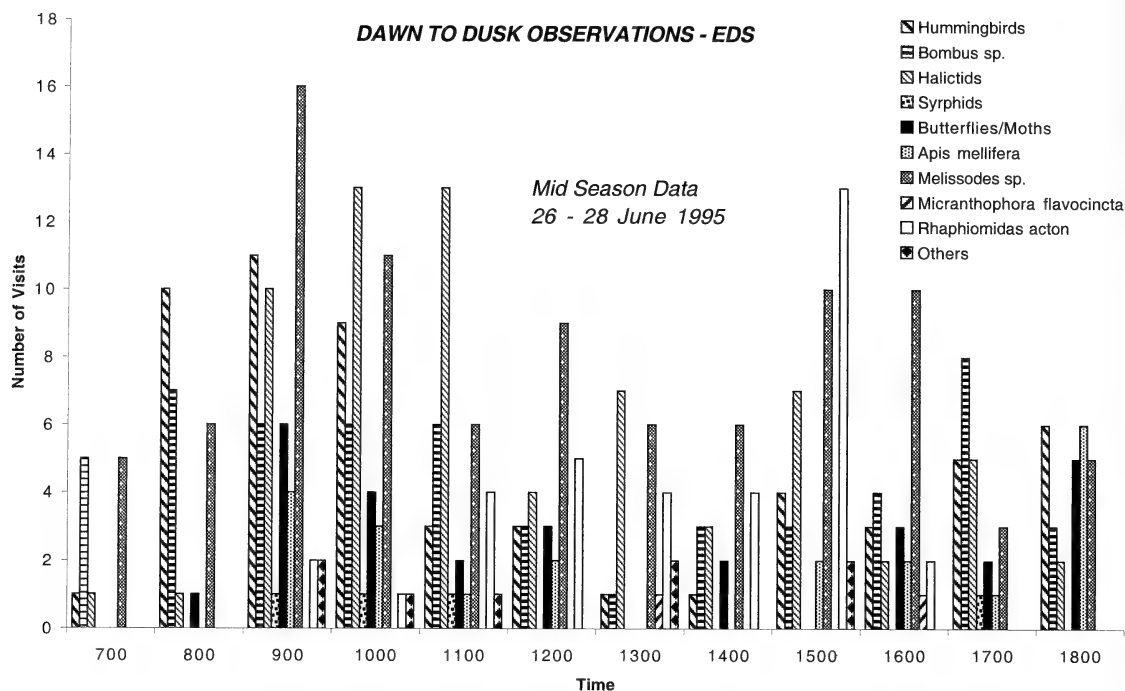
Fig. 3. Observations of pollinators of literally hundreds of flowers on 45–60 large plants of Eds—270 hours of observations were recorded during this period.

son (Fig. 3), and late season (Fig. 4). Data were collected and maintained for most species individually. However, for clarity of presentation, pollinators have been lumped as follows: all hummingbirds, all species of bumblebees (*Bombus* spp), all halictid bees, all syrphid flies, and all butterflies and moths. The minor visitors, including various beetles and wasps, have been grouped together as "other." The remaining pollinators are presented as single-species categories. Overall, the most prevalent pollinators included hummingbirds, species of bumblebees, halictid bees, digger bees (*Melissodes* spp.), and the Giant Flower-loving Fly, *Rhaphiomidas acton.*

Variation did occur among the sampling periods. The most common pollinators during the early season observations were halictid bees, primarily *Halictus tripartitus.* The halictid bees continued to be important pollen vectors throughout the blooming season of *Eds,* but their numbers declined. Digger bees, (*Melissodes* spp.), were relatively common throughout the blooming period, but were particularly prevalent during the mid season. Hummingbirds were important pollinators throughout the entire flowering period. They were typically the predominant pollinators during the morning hours and usually had a smaller, but significant burst of visitation activity in the late afternoon and early evening hours. The Giant Flower-loving Fly, *Rhaphiomidas acton,* became a major contributor to the pollination success of *Eds* during the mid season of

blooming. This species was one of the dominant flower visitors in the afternoon hours.

Nectar rewards. Eds nectar rewards varied considerably within and among the Study Sites (see Table 1). When all the data were combined, the average quantity of nectar was 1.91 μl per flower.

Pollinator constancy. Pollen loads were examined on eight different insect pollinators of *Eds* to determine the relative constancy of each of these insect pollination vectors. Data were pooled for all sites and are presented in Table 2. Using our definition of floral constancy, the only truly constant pollinator was the Giant Flower-loving Fly. The other pollinators show tremendous variability in constancy among the sampled individuals. Note that one of the more important groups of pollinators, the hummingbirds, was not sampled.

Pollinator efficiency. Pollinator efficiency in terms of fruit set for a single touch and for two touches by each of the three primary pollinators, the Giant Flower-loving Fly, bumblebees, and hummingbirds is presented in Table 3. Using a t-test, there were no significant differences found between a single touch and two touches for any of the three principal pollinators tested.

Pollinator efficiency in terms of seed per fruit for a single touch and for two touches by each of these same three primary pollinators is presented in Table 4. Seed set per capsule was the same regardless of

DAWN TO DUSK OBSERVATIONS - EDS

Late Season Data
3, 5 - 6 July 1995

Legend:
- Hummingbirds
- Bombus sp.
- Halictids
- Syrphids
- Butterflies/Moths
- Apis mellifera
- Melissodes sp.
- Micranthophora flavocincta
- Rhaphiomidas acton
- Others
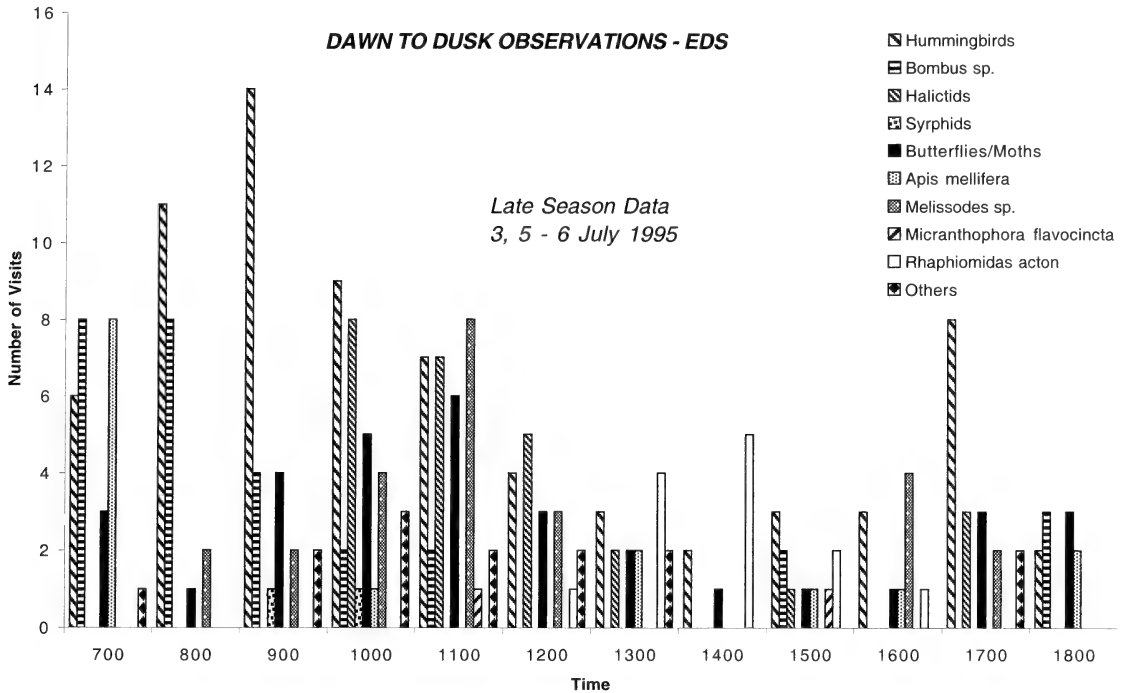
FIG. 4.   Observations of pollinators on literally hundreds of flowers on 45–60 large plants of Eds—270 hours of observations were recorded during this period.

treatment and was not significantly different from the control seed set.

DISCUSSION

A variety of organisms have been shown to be effective pollinators of *Eds:* hummingbirds, bumblebees, halictid bees, digger bees and the Giant Flower-loving Fly (see Tables 3 and 4). Other species have proved to be significant pollinators in previous years including a small bee, *Micranthophora flavocincta* (Munoz 1991) and hawkmoths (Erickson 1993). All of the effective pollinators have "tongues" long enough to reach the nectar reward at the base of the 25–35 mm long floral tubes of *Eds.*

With the diversity of pollinators visiting *Eds,* it would appear that no particular pollinator should be a limiting factor in the reproductive success of *Eds.* However, overall numbers of pollinators can influence reproductive success. Although the spectrum of potential pollinators observed in the most recent studies remained very similar to past observations (See Munoz 1991; Erickson 1993; Stone,

1995; Atallah and Jones unpubl. data), the numbers of individuals of each of these species declined from the numbers observed in dawn to dusk observations in the previous studies. This reduction in the number of individuals of each pollinating species is correlated with a dramatic reduction in seeds per fruit in the 1995 blooming season.

The ovary of each flower of *Eds* has three locules and each locule normally contains five, rarely to six or seven ovules (Harrison 1972; Munz 1974; Hickman 1993). Therefore, each fruit (capsule) has the potential of normally having up to 15 seeds. However, Erickson (1993) found that seed per fruit in open pollinated *Eds* controls at Study Sites 1 and 5 in 1991 averaged 5.74 and 5.8, respectively. An examination of seeds per fruit in open pollinated controls at these same two sites in 1992 resulted in an average seeds per fruit of 3.89 and 4.21, respectively. In contrast, during the 1995 season, average seeds per fruit in open pollinated control flowers, which had been marked in the bud stage (OT), was only 0.94 and 0.91 at Study Sites 1 and 5. Even when compared to a second set of open pollinated

TABLE 1.   AVERAGE NECTAR QUANTITIES PER FLOWER FOR THE *EDS* STUDY SITES.

	Site 1	Site 2	Site 3	Site 4	Site 5
N	150	150	150	150	150
Range (in μl)	0.02–3.81	0.05–5.38	0.04–5.14	0.01–3.97	0.01–4.17
Average μl Nectar Per Flower	1.28	2.99	2.39	1.36	1.49

TABLE 2. POOLED POLLINATOR CONSTANCY DATA FOR 8 MAJOR INSECT POLLINATORS FOR ALL SITES. N = sample size. s = standard deviation. * Sample size too small for valid sample mean or standard deviation calculations.

Species	N	Mean % constancy	Range (%)	s
Bombus californicus	6	40.0	1.4–91.7	36.4
Melissodes communis	17	48.2	9.2–89.5	25.9
Apis mellifera	9	76.2	2.2–100.0	35.0
Micranthophora flavocincta	2	74.9*	52.0–97.8	*
Rhaphiomidas acton	6	94.8	89.1–100.0	3.81
Melissodes sp.	2	27.6*	6.5–48.7	*
Halictus farinosus	1	*	72.6	*
Halictus triparitus	2	79.6*	76.4–82.7	*

unmarked, control flowers that had set fruit and were selected at the time the fruits were collected (ONT), seeds per fruit at Study Sites 1 and 5 for the 1995 season averaged only 3.13 and 1.75 seeds per fruit respectively (Atallah and Jones in preparation). What effect this reduction in reproductive success will have on *Eds* is unknown, but it clearly needs to receive further investigation (Attallah and Jones manuscript in preparation).

An understanding of pollinator constancy helps determine how interdependent a flowering plant is with its pollinator(s). The vast majority of *Eds* pollinators did not show uniform pollinator constancy (see Table 2). Some individuals of most of the pollinators investigated had very pure loads of *Eds* pollen and were quite obviously very constant to *Eds*. Other individuals of the same species, which were also collected while visiting *Eds*, were just as obviously visiting several species of flowering plants on a single foraging flight. The Giant Flower-

loving Fly, *Rhaphiomidas acton*, is the only principal pollinator that uniformly exhibited a very high degree of constancy as measured by the purity (94.8%) of the pollen loads that it was carrying. It appears from our data that the Giant Flower-loving Fly may be monotrophic, meaning that they primarily visit only a single species of flowering plant for all their nectar and/or pollen needs. We have occasionally observed individuals of the Giant Flower-loving Fly visiting flowers of other species of plants in the *Eds* habitat, but this is not a common event.

We were unable to sample any hummingbirds to determine their constancy, but many observations of hummingbirds in the *Eds* habitat indicate that they routinely visit many different flowering plants at the same time that they are visiting *Eds* plants in bloom. These observations lead us to believe that they are also not particularly constant.

Nectar volume per flower varied considerably among the sites and within each site (see Table 1). As nectar volume per flower increases, the length of time spent at a flower by a given pollinator may increase (Montgomerie 1984; Harder 1986; Mitchell and Paton 1990). The inverse should reduce the time spent at a flower by a given pollinator and thus, increase the number of flowers visited. Therefore, it may be advantageous for plants to either reduce the amount of nectar per flower or, at the very least, exhibit considerable variation in nectar production per flower on the same plant and within

TABLE 3. POLLINATOR EFFICIENCIES OF 3 MAJOR INSECT VECTORS IN TERMS OF FRUIT SET (CALCULATED AS PERCENT POLLINATED FLOWERS SETTING FRUIT). Data from all five sites were pooled. ONT: controls that were established using non-tagged flowers from the same inflorescence containing the experimental flowers. 1TF: one touch by a freshly killed, pollen laden Giant Flower-loving Fly. 1TB: one touch by a freshly killed, pollen-laden bumblebee (*Bombus* sp). 1TH: one touch from a pollen-laden head of a stuffed Anna's Hummingbird. 2FT: two touches by a freshly killed pollen laden Giant Flower-loving Fly. 2TB: two touches by a freshly killed, pollen-laden bumblebee. 2TH: two touches from a pollen-laden head of a stuffed Anna's Hummingbird. SD = Standard Deviation. 2SE = Two standard error of the mean. CI = 95% Confidence Interval. n = 25, (exceptions: 1TB, n = 22, for 1TF and 2TB, n = 23, and for 2TF and 2TB, n = 24).

Treatment	Mean (%)	SD	±SE	CI (%)
ONT	94.7	20.8	8.3	86.4–100.0
1TF	72.5	35.8	14.9	57.6–87.4
1TB	80.4	24.5	10.5	69.9–90.8
1TH	54.1	33.9	13.8	40.3–68.0
2TF	63.9	32.6	13.3	50.6–77.2
2TB	82.7	22.2	9.2	73.5–91.9
2TH	74.8	30.9	12.3	62.4–87.1

TABLE 4. POLLINATOR EFFICIENCIES OF 3 MAJOR INSECT VECTORS IN TERMS OF SEED SET PER FRUIT. Data from all five sites were pooled. See Table 3 for an explanation of abbreviations and sample size information.

Treatment	Mean seeds per fruit	SD	±2SE	CI
ONT	4.75	2.3	0.9	3.85–5.65
1TF	4.50	2.9	1.2	3.31–5.69
1TB	5.28	2.9	1.2	4.04–6.52
1TH	3.21	2.7	1.1	2.09–4.33
2TF	3.87	2.7	1.1	2.77–4.97
2TB	5.53	2.5	1.1	4.47–6.59
2TH	3.73	2.4	1.0	2.77–4.69

the population of the species (the latter is certainly the case for *Eds*). Such a strategy should result in an increase in the number of flowers a pollinator visits to achieve a full nectar load. This should increase the number of interplant visits and be advantageous for an obligate outcrosser like *Eds* (Pyke 1978, 1981; Zimmerman 1983).

The three principal pollinators we tested are all reasonably efficient pollinators (see Tables 3 and 4). In terms of fruit and seed set, there were no significant differences between single and dual pollinator visits (touches) for any of these test pollination vectors. This indicates that any one of these principal pollinators could effectively pollinate a flower of *Eds* with a single visit and, as a result, effect full or nearly full fruit and/or seed set when compared to the controls. This further indicates that *Eds* reproduction is not dependent on any single pollination vector.

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DEMOGRAPHY AND POPULATION BIOLOGY OF A RARE TARPLANT, *BLEPHARIZONIA PLUMOSA*, (ASTERACEAE) A CALIFORNIA SUMMER ANNUAL FORB

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ABSTRACT

Blepharizonia plumosa (Kellogg) E. Greene, also known as the big tarplant, is a rare, summer-flowering, annual tarplant found in California grasslands. Although rare throughout its range, *B. plumosa* is numerous at the Lawrence Livermore National Laboratory (LLNL) experimental test facility, Site 300. We conducted a common garden experiment, a reciprocal transplant study, and a laboratory germination study to compare *B. plumosa* to its more common relative, *B. laxa* Greene (which is rare at Site 300), and to gather data on the basic biology of *B. plumosa* in preparation for a possible mitigation project. Three populations of *B. plumosa* were compared to a single population of *B. laxa*. Little population differentiation was found in *B. plumosa* in terms of transplant success. *Blepharizonia plumosa* expresses much more extreme dimorphism with respect to seed germination: ray seeds have low germination percentages (<4%) compared to disc seeds (50–78%, P < 0.017). *Blepharizonia laxa* did not show any significant differences between ray (18%) and disc (17%) seed germination (P > 0.05). *Blepharizonia plumosa* produced three times more ray seeds than disc seeds (ratio: 3.2), while *B. laxa* produced little over half as many ray seeds as disc seeds (ratio: 0.65). *Blepharizonia plumosa* plants grown from ray seeds have a lower biomass accumulation (<5 g per plant compared to 28 g per plant for *B. laxa*, P < 0.017) and none survived to flower production. Among ray-derived *B. laxa* plants, 70% survived to flower production. This difference in ray seed production and performance points to a possible basis for ecological differences between the two species. Until the mechanisms controlling dormancy are more clearly understood, only disc seeds should be used in the creation of new populations of *B. plumosa*.

Annual plants within California grassland communities are often divided into functional groups based on their flowering period, e.g., early grasses, late grasses, early forbs, and summer forbs (Pendleton et al. 1983). Due to the changes in climate throughout the growing season, plants within these groups are confronted with a wide range of environmental conditions, e.g., changing soil moisture content and photoperiod. Compared to the early spring flora, relatively little ecological information appears to be available on the annual summer forbs. These summer forbs, or late forbs, include species of the tarplant subtribe *Madiinae* (Compositae), e.g., *Hemizonia, Madia,* and *Calycadenia,* as well as *Blepharizonia.* Information on species in the summer flora is important for conservation and habitat restoration activities. For example, 110 late-flowering (July–September) taxa listed by the California Native Plant Society (CNPS) are of conservation concern. Of these, eight taxa are state or federally listed as threatened or endangered (Skinner and Pavlik 1994).

The flowering period of summer forbs, such as *Hemizonia* (Chiariello 1989) and *Blepharizonia* (personal observation), starts in late July or early August and can extend into November. Because of their late-flowering period, summer forbs spend much of their lifetime in the harsh California summer drought. They are able to survive drought conditions by developing deep root systems and are able to escape the higher temperatures that occur at the soil surface due to their height (Morse 1988). In water usage studies conducted by Gulman et al. (1983), it was found that a spring-flowering plant (*Clarkia*) and a summer-flowering plant (*Hemizonia*) differ in their access to stored water in the post-precipitation season. *Hemizonia* has the ability to root into deeper non-nutritive substrate for water, while *Clarkia* cannot. In addition to being able to access additional water, summer flowering plants postpone water stress through hydrophilic, pectinaceous, extracellular polysaccharides concentrated in leaf tissue (Morse 1988) and are able to flower at lower water potentials (Chiariello 1989). Schoenherr (1992) points out that by postponing the flowering stage into the summer months, summer forbs have less competition for pollinators.

Later-blooming plants accumulate an order of magnitude more biomass than earlier-blooming plants (Mooney et al. 1986) and may also have some additional colonization advantages. First, naturally disturbed sites, such as gopher mounds, can be ideal for colonization. The later a species flowers, the larger the number of mounds available. Second, since late-flowering species tend to be taller than spring-flowering species, their seeds

have a wider dispersal radius. This allows them to colonize mounds and other disturbed areas farther from their immediate neighborhood (Hobbs and Mooney 1985).

Blepharizonia plumosa (Kellogg) E. Greene is an extremely rare late-flowering plant included on the CNPS List 1B (Skinner and Pavlik 1994, under the former moniker *Blepharizonia plumosa* subsp. *plumosa*[1]), which includes plants that are rare, threatened, or endangered. The CNPS R-E-D code (rarity-endangerment-distribution) for *B. plumosa* is 3-3-3, which indicates that this plant is limited to one or several restricted populations, is endangered throughout its range, and is endemic to California. The CNPS also noted that possibly the only remaining populations exist on private property in the hills near Livermore, California. Populations have been previously identified in Alameda, Contra Costa, San Joaquin, Stanislaus, and Solano Counties (Skinner and Pavlik 1994). Preston (1996) noted that a population was discovered at Contra Loma Regional Park, south of Antioch in 1979, but that surveys conducted by the East Bay Regional Park District in 1991 were unable to relocate the species. In 1994, several more populations were discovered on private property southwest of Brentwood (CNDDB 1996). Another small population was found at Chaparral Springs near Mount Diablo (Preston 1996). Current status of these populations is unknown.

Several populations of *B. plumosa* were identified during a habitat survey in 1996 at Lawrence Livermore National Laboratory's (LLNL) experimental test facility (Site 300). A few populations of the more common big tarplant, *Blepharizonia laxa* Greene, were also found. *Blepharizonia laxa,* although also endemic to California, exists in plentiful numbers and has a much larger range which extends farther south into the inner South Coast Ranges, including San Benito County (Hickman 1993). Site 300 is a high-explosive test site operated by the University of California for the Department of Energy. The site is closed to the public and has had no agricultural activity since its establishment in the 1950s. The botanical diversity of the site may be due to its lack of public access, lack of agricultural activity, and high burn frequency. Large stands of the native perennial bunchgrass, *Poa secunda* J.S. Presl, occur in the northern portion of the site and are thought to be maintained by the annual late spring/early summer controlled burns conducted for wildfire control (Carlsen et al. 2000). The large-flowered fiddleneck, *Amsinckia grandiflora* A. Gray (Boraginaceae), which is on the state and federal endangered species lists

(Schoenherr 1992), and the diamond-petaled poppy (*Eschscholzia rhombipetala* E. Greene), which was until recently thought to be extinct (Hickman 1993), are both found at Site 300. While historical occurrences of many rare plants probably have been extirpated by agricultural activities and non-native plant colonization (Skinner and Pavlik 1994), these factors may be reduced at Site 300.

While the rarer taxon, *B. plumosa,* is quite common at Site 300, occurring most plentifully in areas that are routinely burned, *B. laxa* is uncommon at Site 300, but exists in both unburned and burned areas. The two species are known to co-occur at only two locations, one of which is routinely burned. That the two species appear to differ in their habitat requirements may indicate some ecological differences between them. Comparison of rare and common congeners can provide important information for rare plant management (Pantone et al. 1995) and can illuminate differences that affect comparative abundance (Byers 1998).

For conservation and management purposes, a thorough understanding of the population dynamics and the feasibility of population restoration of *B. plumosa* are critical. Mitigation of a *B. plumosa* population may need to be performed at Site 300 in the future, but few reintroduced populations of endangered species appear to be self-sustaining (Pavlik 1994; Parsons and Zedler 1997; Pavlik and Espeland 1998). Allen (1994) stated that only four of the 45 reintroduction projects undertaken in California during the past decade were successful when judged by survival and reproduction. In many instances, reintroduction failure was attributed to poor planning or lack of information about the species (Hall 1986; Pavlik 1994). Population restoration is often performed without regard to the level of microhabitat adaptation in source populations (Knapp and Rice 1994). Small-scale adaptation in source populations can prevent success in restoration attempts (Dyer and Rice 1997). However, in situ population differentiation is not necessarily negatively correlated to transplant success (Meagher et al. 1978); thus each of the three *B. plumosa* populations were compared for transplantability in our experiment.

We initiated a study in November of 1996 to collect basic demographic and population biology data on *B. plumosa.* The study was needed to determine if population differentiation in *B. plumosa* occurs with respect to transplant success and also to examine differences between *B. plumosa* and the more common big tarplant, *B. laxa.* The study included a common garden experiment followed by a field reciprocal transplant study to investigate field germination rates. In addition, a laboratory germination study was conducted to investigate the relationship between seed type, seed age, and germination/dormancy. Because so little is known about population biology of *B. plumosa,* and because ongoing activities at Site 300 could poten-

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[1] The *Blepharizonia* genus has recently been revised (Baldwin et al. 2001): *Blepharizonia plumosa* was formerly *B. plumosa* subsp. *plumosa* (Hickman 1993), while *Blepharizonia laxa* was formerly *B. plumosa* subsp. *viscida* (Hickman 1993).

tially impact the populations there, these data could be used both to improve management practices and to prepare for a possible onsite mitigation project at Site 300.

Materials and Methods

Study species. Both *B. plumosa* and *B. laxa* are dicots within the family Asteraceae, and members of the tribe Helenieae (Karis and Ryding 1994). They are both summer annual forbs, which germinate with the onset of the first substantial fall/winter rains and flower July–October. One of the common attributes to this family is heterocarpy, or the production of two or more single-seeded fruit types (achenes) on a single plant. Although the term "seed" should be used when addressing germination and dormancy, and fruit or achene should be used when addressing morphology, the term "seed" will be used solely throughout this paper. In the case of *Blepharizonia,* the plants have dimorphic flowers within the same inflorescence. Seed dimorphism is very common in the plant kingdom, found in the families such as Asteraceae, Chenopodiaceae, Poaceae, Brassicaceae, and is often associated with arid or disturbed environments (Harper 1977; van der Pijl 1972). As discussed by Bremer (1994), seed morphology is among the most important and useful features in Asteraceae classification at the generic and species levels.

The two species can be distinguished from one another by seed morphology and leaf color (Hickman 1993; Baldwin et al. 2001). The most distinctive characteristic of *B. plumosa* is the pappus on the disc seed that is 1.5–3 mm in length. The disc seed pappus is sometimes described as plumose (thus the specific epithet *plumosa*) and contrasts with the very minute pappus of the ray seeds (Fig. 1). The plants also have a pale green color, as their foliage is sparsely glandular below the inflorescence. Older plants have many inflorescences on side branches.

The disc and ray seeds of *B. laxa* appear much more similar to the naked eye and have a short pappus from 0–1 mm in length. *Blepharizonia laxa* is much more glandular than *B. plumosa* giving the plant a more yellow-green color and a much stronger scent. *Blepharizonia laxa* also tend to be slightly taller than *B. plumosa* (personal observation). Older plants have inflorescences mostly terminal on slender wand-like, bracted peduncles (Hickman 1993).

Study site. Corral Hollow is a valley of the Inner Coast Ranges that contains examples of native plants and animals characteristic of the Great Central Valley. This area has been used primarily for grazing sheep and cattle (Schoenherr 1992). Site 300 covers 2711 ha and is located in the Altamont Hills of the Diablo Range separating the Livermore and San Joaquin Valleys. The southern portion of Site 300 (T3S R4E sect. 29 SW ¼) extends into

Corral Hollow and consists of rugged north/south-trending canyons of elevations ranging from 150 m to over 500 m. It is primarily a grassland-dominated site, with sparse populations of coastal sage scrub and blue oak woodland in the southwest corner of the site.

Three populations of *B. plumosa,* designated B834 Berm, B834 Drainage, and B850, and one population of *B. laxa,* designated Middle Canyon, were used in this study. Figure 2 shows Site 300 and the locations of the study populations. Table 1 includes some habitat characteristics of all four populations.

Common Garden Experiment

Intact inflorescences containing seeds were collected in October and November 1996 from the three populations of *B. plumosa* and the single population of *B. laxa.* Following collection, they were segregated into disc and ray seeds. A large container of soil (approximately 60 liters) was also collected in November 1996 from each of the four population sites. No attempt was made to insure the soil was free from existing seeds. A fifth container was filled with potting soil. Each container was divided into four quadrants, each of which was then divided in half. Each quadrant was assigned a source population and its two sub-quadrats delineated disc and ray seeds. In late November 1996, 25 disc and 25 ray seeds from each population were planted into adjacent sub-quadrants in each container, as shown in Fig. 3. Germination was allowed to occur naturally following rainfall events, although all containers were later outfitted with a drip irrigation system to ensure even watering. Germination and growth were closely monitored for approximately 10.5 months, until October 1997. Other species that germinated within the pots were removed. Any *B. plumosa* or *B. laxa* plants that emerged in locations not associated with the planting arrangement were also removed. Seeds were collected from plants as they matured and biomass was collected after senescence.

Data analysis. Percent germination for disc and ray seeds was calculated by population in each of the soil types. To determine if differential germination was occurring, the average percent germination for all seeds planted in native soil ($n = 4$) was compared to that of all seeds planted in non-native soil ($n = 12$). Because no significant relationship was found between soil type (native vs. non-native) and the amount of germination ($P > 0.95$) or percent survivorship ($P > 0.19$), each pot was treated as a replicate for all further data analyses. Percent germination for seed type was calculated by dividing the final number of germinated seeds by the total number planted ($n = 25$). Then, the average percent germination was calculated by taking the mean across all replicates ($n = 5$). The percentage of plants surviving to flower production

Disc

Ray

Common Tarplant, *Blepharizonia laxa*

Disc

Ray
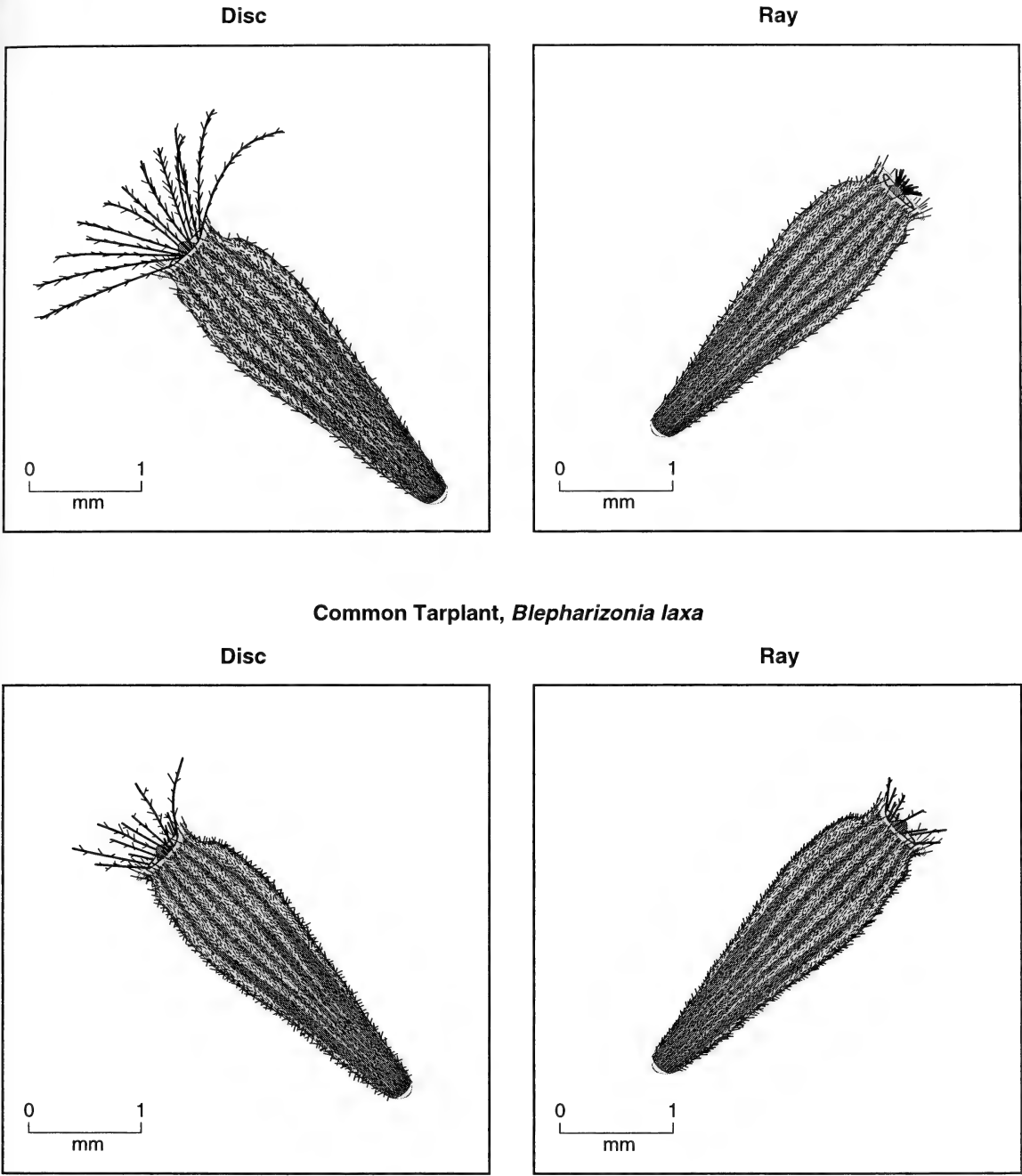
Fig. 1. Comparison of pappus on seeds of *Blepharizonia plumosa* and *B. laxa.*

was calculated by dividing the number of flower-producing plants by the number of plants that germinated, then averaging across replicates (n = 5). Average seed production per plant is the total seed production per replicate divided by the number of plants of the parent seed type in that replicate that produced mature seeds. All five replicates were then averaged. Statistical analysis of seed production was performed on the ratio of ray to disc seeds

that each plant produced. Average biomass was calculated by summing the dry weights (in grams) of the plants collected in each replicate divided by the number of plants, then taking the mean across all replicates (n = 5).

Statistical analyses were performed using the general linear model in SAS, version 6 (SAS 1990). All percentage data were arcsine transformed prior to analyses. Single degree of free-
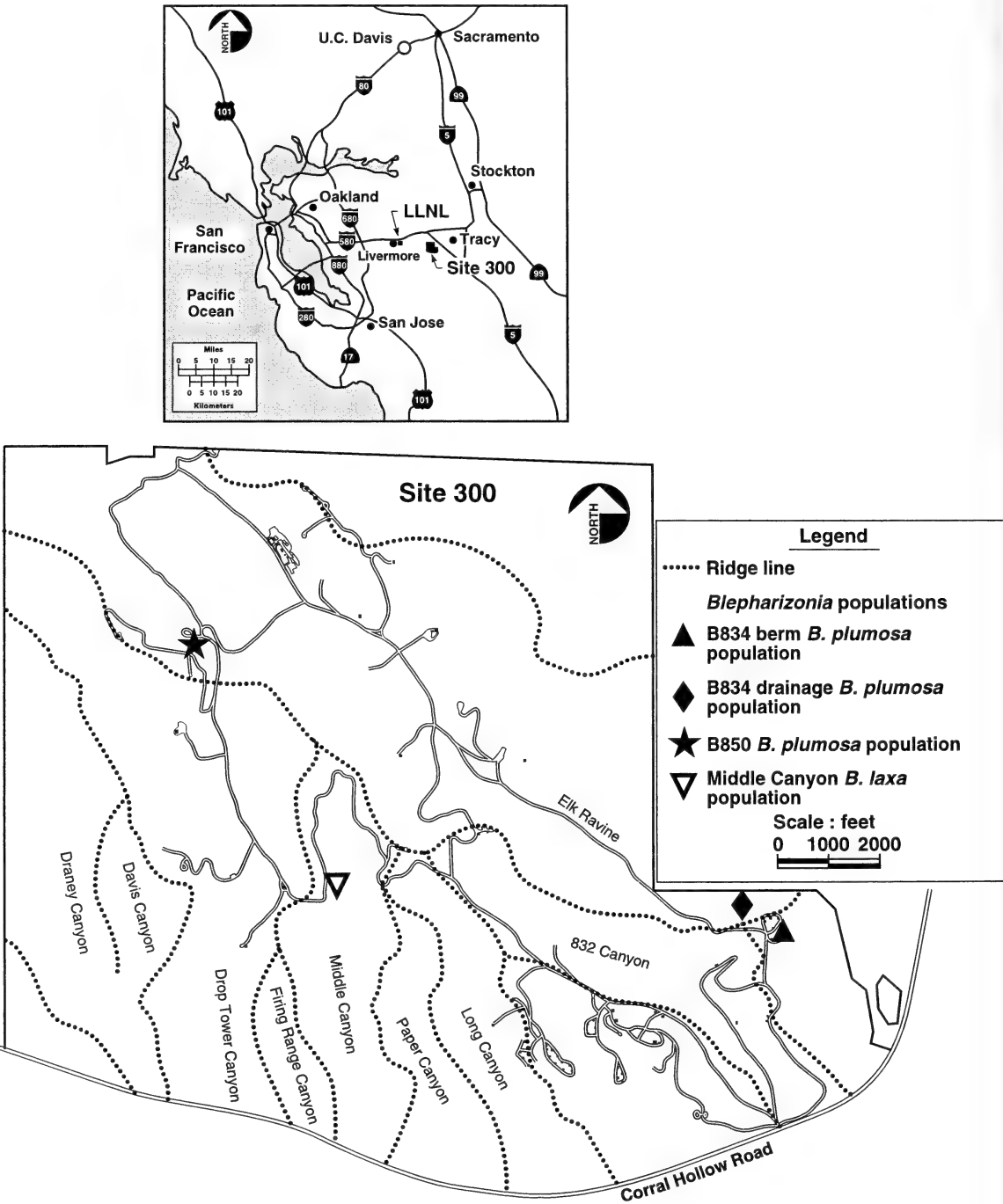
FIG. 2. Site 300 and locations of *Blepharizonia plumosa* populations.

dom f-tests (orthogonal contrasts) were per-formed to ascertain if differences occurred be-tween disc and ray seeds within each species and then if differences occurred between the two spe-cies within each seed type. Tukey's separation of means was performed to determine if populations of *B. plumosa* were different from each other. Be-

cause of the multiple tests performed on the same data sets, a corrected alpha value was used to determine significance. Using a Bonnferroni cor-rection, we divided our starting alpha value of 0.05 by three (the number of comparisons per-formed upon each dataset), so a test would have to have a P value of less than 0.017 to be signif-

Table 1. Habitat Characteristics of Three *Blepharizonia plumosa* Populations and one *B. laxa* Population at Site 300 (Adapted From Preston 1996).

Population	Number of plants	Plant community	Elevation (m)	Aspect	Slope (%)	Soil type	Management practices
B834 Berm (*B. plumosa*)	≈200	exotic annual grassland, *Avena* sp., *Gutierrezia californica, Eriogonum angulosum, Bromus diandrus, Holocarpha obconica*	≈315	north	8–30	clay, Alo-Vaquero complex	not burned, berm with low grass cover
B834 Drainage (*B. plumosa*)	500–1500	exotic annual grassland, *Bromus hordeaceus, B. diandrus, Amsinckia intermedia, B. madritensis* ssp. *rubens, Grindelia camporum.*	≈215	north	50–75	sandy to clay loam, Wisflat-Arburua-San Timoteo complex	annually burned
B850 (*B. plumosa*)	≈100	disturbed annual grassland, *Avena* sp., *Bromus madritensis* ssp. *rubens, Vulpia myuros*	≈400	north	30–50	rocky sand to clay loam, Wisflat-Arburua-San Timoteo complex	annual burned
Middle Canyon (*B. laxa*)	not determined	exotic annual grassland, *Avena* spp., *Bromus diandrus, B. rubens, B. hordeaceus, Hordeum marinum, Silybum marianum, Marah fabaceus, Gutierrezia californica, Phacelia distans*	≈400	east	50–75	sandy to clay loam, Wisflat-Arburua-San Timoteo complex	not burned

icant. This correction decreases our chance of rejecting the null hypothesis erroneously.

Reciprocal Transplant Study

Four 100-m² plots were established within each of the three *B. plumosa* populations. Disc and ray seeds from the common garden experiment were used in this study. As shown in Fig. 4, seeds were planted five across in four rows, each row corresponding to one of the four populations. Each plot was subdivided; one subdivision was assigned to disc seeds and the other to ray seeds. The seeds were spaced 11–12 cm apart within each row, each row was spaced six to seven cm apart, and each subdivision was spaced 11–12 cm apart. Seeds were planted in all four plots in each of the three *B. plumosa* populations. At the time of planting, seed placement was marked using colored plastic straws 10 cm in length. Upon germination, the seedlings were marked by placing a circle of string loosely around the base of the plant. The germination rate, growth, and survival of all marked plants were monitored throughout the season.

Data analysis. There was no difference in germination between locations for any parent population (P = 0.544), so data from all locations were pooled for analysis. Percent germination was calculated for each plot by source population and seed type. The individual plot values were then averaged (n = 4). Finally, the mean for the three populations or transplant locations was found (n = 3). Statistical analyses were performed in the same manner as those for the common garden study.

Laboratory Germination Study

Inflorescences were collected from the three *B. plumosa* populations and the *B. laxa* population in 1996, 1997, and 1998, and from the common garden experiment pots in 1997. All were collected in autumn (September–November) at the predispersal stage. The material was sorted into disc and ray seeds and stored at room temperature. Only seeds that appeared to be undamaged and fully mature were selected for use in the germination study. The seeds selected from the 1996 and 1998 collections were taken from native populations. However, due to the limited number of suitable seeds collected from the native populations in 1997, seeds from the common garden experiment were used for this year. For the *B. plumosa* populations, three replicates of 20 ray seeds and three of 20 disc seeds were used. Six replicates of 20 ray seeds and six of 20 disc seeds were used for the *B. laxa* population. Germination was initiated on 30 Nov 1998 for seeds collected in 1996 and on 1 Dec 1998 for seeds collected in 1997 and 1998. Seeds were placed in plastic Petri plates on Whatman 80 filter paper moistened with deionized water. The plates were then sealed with parafilm to reduce water evaporation
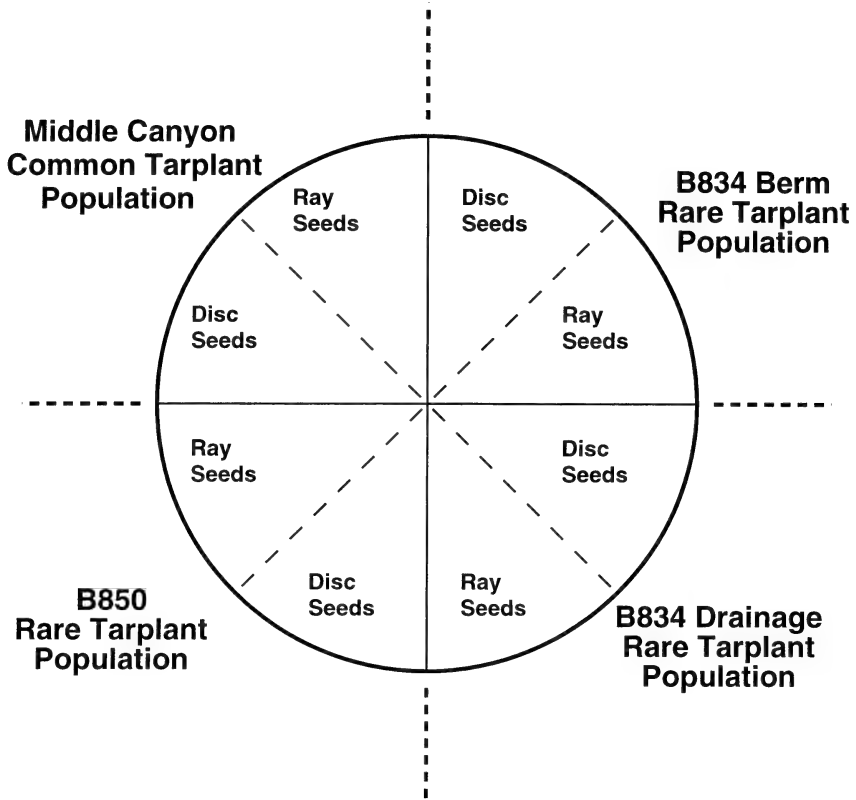
FIG. 3. Planting arrangement of tarplant seeds within each of five containers in the common garden experiment.

and placed in a dark cooler kept at room temperature. Germination data were collected for approximately six weeks (43 days) following initial wetting of the plates. All plates were wet again at the end of Week 1 (Day 8) and Week 2 (Day 16). At the end of Week 4 (Day 36), 60 percent of the plates were rewet as necessary. Germinules were removed as they germinated to control for any possible post-germination effects.

Data analysis. Percent germination was found by dividing the number of germinated seeds by the total number of seeds in the plate. Because some of the seeds selected were later determined to be immature, the number of seeds per plate ranged from 13 to 20. The seeds that did not germinate were examined under a dissecting microscope at the end of the experiment and designated as immature if they lacked an embryo. The individual plate values were then averaged by seed type, population, and year (n = 3 for *B. plumosa,* n = 6 for *B. laxa*). Cumulative germination represents final percent germination values. Final germination percentages were arcsine transformed and analyzed for age and subspecies effects using the general linear model in SAS, version 6 (SAS 1990). Fruit age (0, 1, or 2 years) was plotted against final percent germination for ray and disc seeds in *B. plumosa* and *B. laxa*

using a least-squares linear regression (SAS 1990). Because three analyses were run on the same dataset (linear regression by species and by seed type plus a general linear model), our corrected alpha value was 0.05 divided by 3 to determine our significant P value (0.017).

RESULTS

Common Garden Experiment

Table 2 presents the results and statistical analyses of the germination rates, survivorship, and biomass production for the common garden experiment. A dramatic difference was observed in percent germination between the disc seeds and ray seeds for *B. plumosa.* Germination of the *B. plumosa* disc seeds ranged from 50 to 78%, while ray seed germination was below 4%. No statistical difference was observed between disc and ray germination for *B. laxa.* Although *B. plumosa* disc seeds appeared to have a higher level of germination than those of *B. laxa* disc seeds, and the inverse was true for ray seeds, due to the small sample size and high amount of variability within the *B. laxa,* these differences were not significant. A priori comparisons showed that there were no differences between *B. plumosa* populations for ray and disc germination.
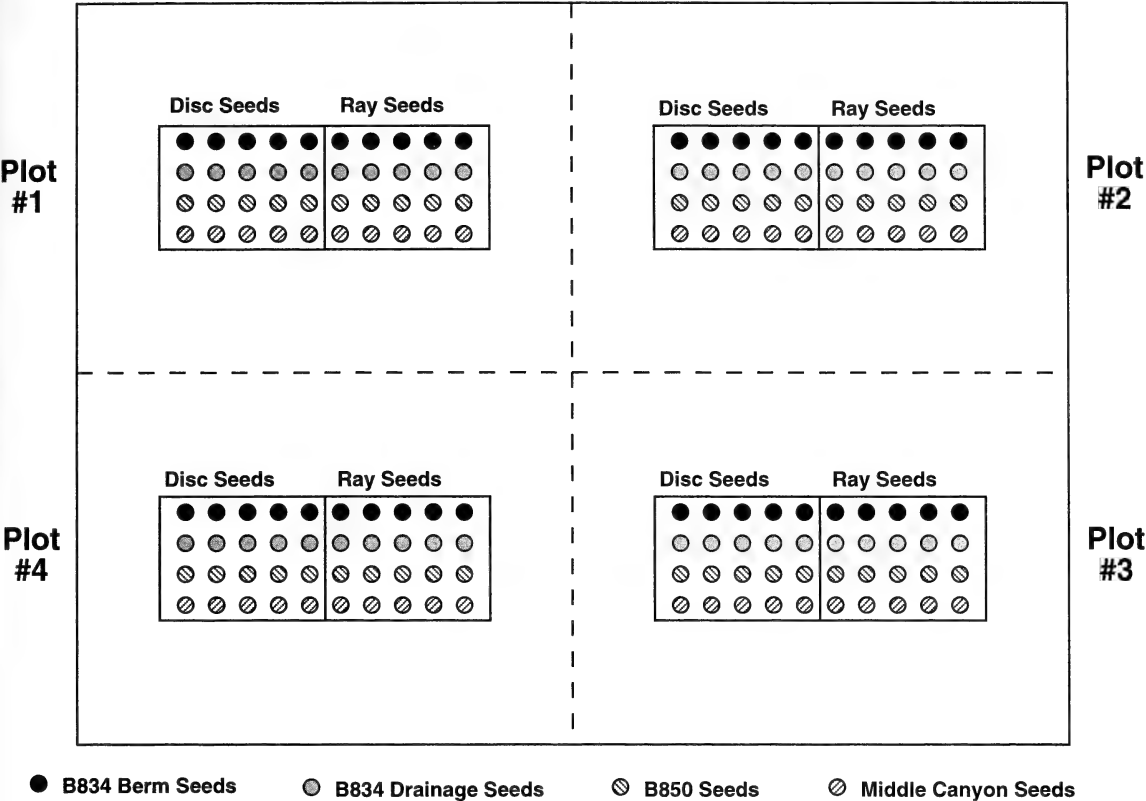
FIG. 4.   Diagram of reciprocal transplant study within each of three tarplant field populations.

When comparing the percentage of tarplants surviving to flower production in the common garden experiment, a survivorship difference was apparent between the disc- and ray-seed derived plants for the *B. plumosa*. No ray-derived *B. plumosa* plants survived to flowering. However, because of the large difference in sample size (n = 7 ray-seed derived plants compared to n = 231 disc-derived plants) statistically significant differences were not found. No significant difference in survivorship was found between disc- and ray-derived *B. laxa* plants. Also, no difference in survivorship was found between *B. plumosa* and *B. laxa* disc-derived plants. However, a significantly lower percentage of *B. plumosa* ray-derived plants survived to flower production when compared to *B. laxa* ray-derived plants. As already mentioned, none of the *B. plumosa* plants from ray seeds survived, while 70% of *B. laxa* plants from ray seeds survived to flower production (n = 9). A priori comparisons showed that there were no differences in survivorship between *B. plumosa* populations.

When comparing biomass production, no difference per plant between disc- and ray-derived plants was found in either *B. laxa* or *B. plumosa*. The *B. laxa* plants, however, achieved much higher biomass (average 28 g) for ray-derived plants than *B.*

plumosa ray-derived plants were able to accumulate (each plant less than 5 g).

The average seed production per plant is shown in Figure 5. Statistical analyses found an interaction between parent morph and seed morph ratio for *B. plumosa* and *B. laxa* (P < 0.0005). The ratio of ray to disc seed production from disc-derived *B. plumosa* plants was 3.2, while the ratio from the disc-derived *B. laxa* plants was 0.65, meaning that more similar numbers of disc and ray seeds were produced from the *B. laxa*. Again, no seeds were produced by the ray-derived *B. plumosa* (none survived to reproductive maturity). Ray-derived *B. laxa* produced many more disc seeds (average = 185) than ray seeds (average = 59). Several of the disc-derived *B. laxa* plants died prior to complete maturation of the seeds, which may account for the low numbers of seeds produced by these plants.

Reciprocal Transplant Study

The results and statistical analyses for germination rates in the reciprocal transplant study are presented in Table 2. As in the common garden experiment, a significantly higher amount of germination was observed for disc seeds than for ray seeds for *B. plumosa,* but no difference was observed between disc and ray germination for *B.*

TABLE 2. GERMINATION, SURVIVORSHIP, AND BIOMASS RESULTS OF THE RECIPROCAL TRANSPLANT AND COMMON GARDEN EXPERIMENTS (AVERAGE ± 1 SE). Differential shading between ray and disc categories indicates significant difference at P < 0.017 in the rare tarplant (*B. plumosa*). [a, b, ab] Different lowercase letters indicate significant differences among *B. plumosa* populations for disc seeds at P < 0.017. [A, B, AB] Different uppercase letters indicate significant differences among *B. plumosa* populations for ray seeds at P < 0.017. [*, **] Different symbol repetitions indicate significant differences between species for disc seeds at P < 0.017. [#, ##] Different symbol repetitions indicate significant differences between species for ray seeds at P < 0.017.

| | | Common garden | | | Reciprocal transplant |
		% germination	% survivorship	Average biomass (g)	% germination
B834 Berm					
B. plumosa	Disc	$77.6 + 5.46^{a*}$	$33.4 \pm 14.0^{a*}$	$2.28 \pm 0.54^{a*}$	$35.00 \pm 11.55^{a*}$
	Ray	$1.6 \pm 0.98^{A\#}$	$0 \pm 0^{A\#}$	$0 \pm 0^{A\#}$	$3.3 \pm 1.67^{A\#}$
Ratio (Ray:Disc)		0.021	0	0	0.094
B834 Drainage					
B. plumosa	Disc	$49.6 + 0.98^{a*}$	$49.8 \pm 15.2^{a*}$	$3.04 \pm 0.73^{a*}$	$65.00 \pm 2.89^{b*}$
	Ray	$0.8 \pm 0.8^{A\#}$	$0 \pm 0^{A\#}$	$4.71 \pm 0^{A\#}$	$1.7 + 1.67^{A\#}$
Ratio (Ray:Disc)		0.016	0	1.549	0.026
B850					
B. plumosa	Disc	$57.6 + 6.27^{a*}$	$48.8 \pm 18.0^{a*}$	$4.00 \pm 1.59^{a*}$	$43.33 \pm 4.41^{ab*}$
	Ray	$3.2 \pm 1.5^{A\#}$	$0 \pm 0^{A\#}$	$0.36 \pm 0.09^{A\#}$	$0 \pm 0^{A\#}$
Ratio (Ray:Disc)		0.056	0	0.090	0
Middle Canyon					
B. laxa	Disc	$23.2 \pm 0.8^{*}$	$58.2 \pm 14.7^{*}$	$7.14 + 2.04^{*}$	$16.70 \pm 6.01^{*}$
	Ray	$7.2 \pm 2.65^{\#}$	$70 \pm 20^{\#\#}$	$27.82 \pm 10.97^{\#\#}$	$18.30 \pm 7.26^{\#}$
Ratio (Ray:Disc)		0.310	1.203	3.896	1.096

laxa. Once again, although higher levels of germination were apparent for *B. laxa* ray seeds when compared to *B. plumosa* ray seeds, and the inverse seemed to be true for disc seeds, these differences were not significant (P = 0.049 and 0.057, respectively). The level of germination of disc seeds from the B834 Berm population was significantly greater than was disc germination from the Drainage population. Otherwise, no population differences were found in germination for *B. plumosa.*

All of the plants in the B850 and B834 Drainage populations were lost during the annual spring controlled burns at Site 300. B834 Berm was not burned, but only five *B. plumosa* and three *B. laxa* plants survived to the flowering stage. All eight were disc-derived plants. Because of the limited sample size, we did not perform statistical analyses of the growth and survivorship data.

Laboratory Germination Study

Germination appears to be related to seed age (Fig. 6). A statistical interaction was found among seed age, seed morph, and parent species (P < 0.0001). Overall disc germination was greater than overall ray germination, and germination in *B. plumosa* tended to be higher than for *B. laxa*. Linear regression performed for each seed type of each species yielded a significant correlation between seed age and germination for disc seeds in both *B. plumosa* and *B. laxa* (Table 3). The regression for *B. plumosa* disc seeds shows a negative slope: germination decreases slightly as seed age increases. *Blepharizonia laxa* disc seeds show the opposite trend where increasing seed age correlated to a small increase in germination. *Blepharizonia plumosa* ray seeds also show a slight increase in germination with increasing seed age, while germina-
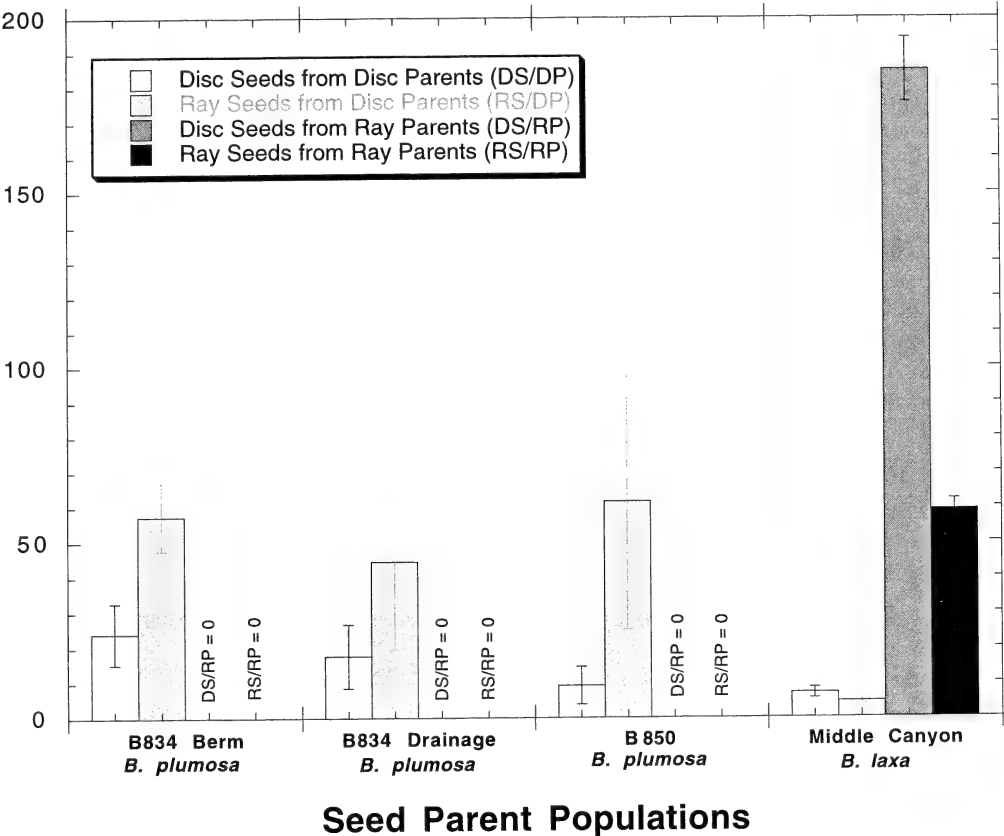
FIG. 5.   Average number of mature disc and ray seeds produced from each parent seed type plant (n = 5, error bars = 1 SE).

tion for *B. laxa* ray seeds did not show any significant changes with increasing age.

DISCUSSION

Germination rates and dormancy. The common garden, reciprocal transplant and laboratory germination experiments showed extreme dimorphism in germination percentages of disc and ray seeds within *B. plumosa*, while little dimorphism was found for *B. laxa*. This dimorphism seems to be a common phenomenon within Asteraceae, e.g., in *Heterotheca subaxillaris* var. *subaxillaris* (Baskin and Baskin 1976), *Heterotheca grandiflora* Nutt. (Flint and Palmblad 1978), *Holocarpha macradenia* (DC.) E. Greene (Palmer 1982), *Senecio jacobaea* (McEvoy 1984), *Heterotheca latifolia* (Venable and Levin 1985), *Hemizonia increscens* (Keck) B.D. Tanowitz (Tanowitz et al. 1987), *Heterosperma pinnatum* (Venable et al. 1987), and *Hedypnois rhagadioloides* (Kigel 1992). In all of these studies, disc seeds germinated more rapidly and in higher final proportions than did ray seeds. However, to our knowledge, we are the first to report differences in germination from ray and disc seeds between two closely related species within Asteraceae. These different germination responses are fairly

subtle, and the implications are not fully known. Although seed dimorphism is often associated with different germination responses (Esashi and Leopold 1968; Baskin and Baskin 1976; Flint and Palmblad 1978; McEvoy 1984), few have attempted to determine how laboratory results correspond with germination characteristics in the field (Tanowitz et al. 1987).

It has been demonstrated that disc seeds exhibit either no dormancy or significantly shorter dormancy periods in comparison to ray seeds, which exhibit dormancy in all species mentioned above. Several causes of delayed germination for ray seeds have been examined. The most prominent effects on ray seed germination are observed when the pericarp and seed coat are damaged or removed (Palmer 1982; McEvoy 1984; Tanowitz et al. 1987). In these studies, no significant differences were observed in germination rates and final germination proportions between disc seeds and excised ray embryos. McEvoy (1984) suggested that the thick pericarp of the ray seeds acts to physically inhibit germination. However, Palmer (1982) noted that if left intact, the inner nucellar layer (a clear, membranous material) would inhibit germination, potentially acting "in a metabolically active way."
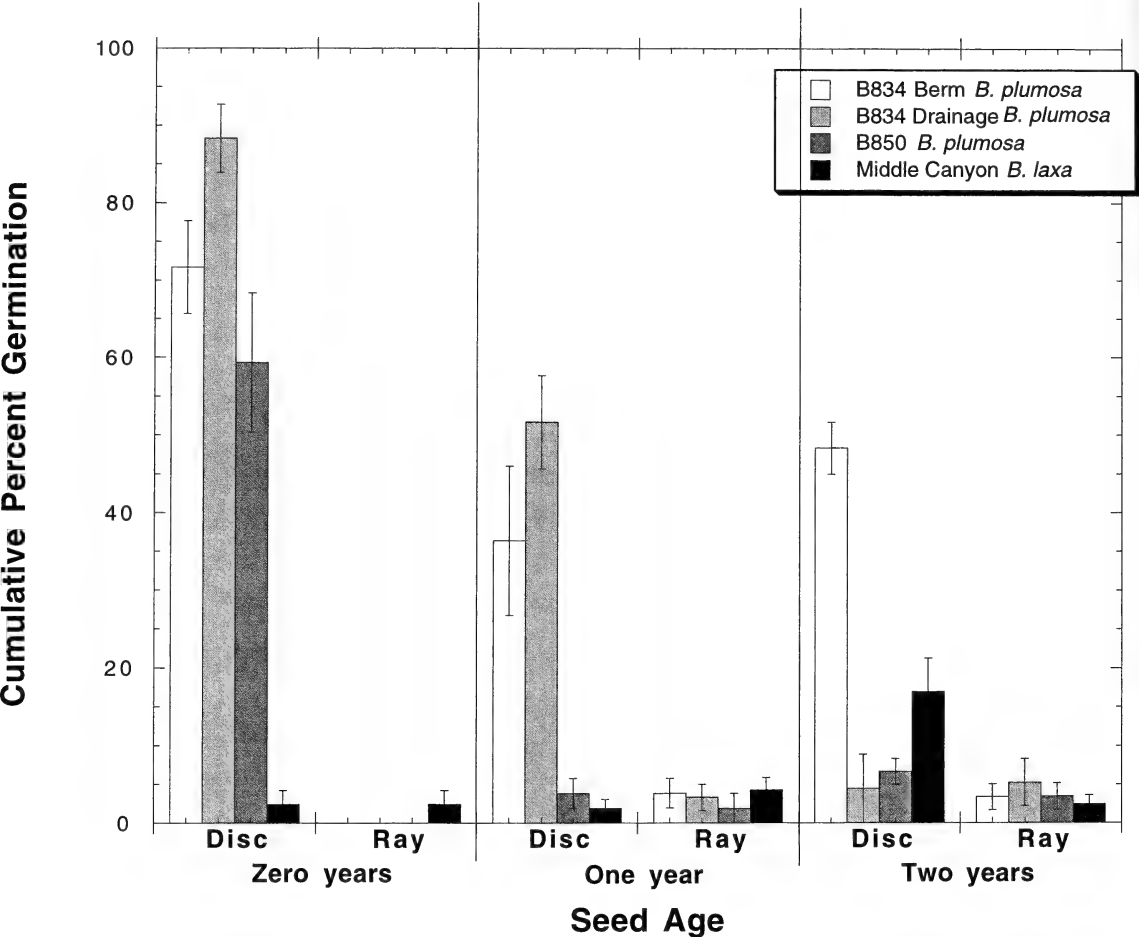
Fig. 6. Germination of disc and ray seeds in the laboratory germination study from three source years (n = 3 for *Blepharizonia plumosa*, n = 6 for *B. laxa*, error bars = 1 SE).

In all cases, the embryos of ray seeds are not dormant, but rather have dormancy imposed on them by maternal tissues (Palmer 1982; McEvoy 1984; Tanowitz et al. 1987).

Multiple environmental factors have been found to influence germination in ray seeds to a greater extent than they influence germination in disc seeds. In several studies, germination of ray seeds was inhibited by darkness, while light availability had little or no effect on disc seed germination (Baskin and Baskin 1976; Flint and Palmblad 1978; Venable and Levin 1985; Venable et al. 1987; Kigel

1992). Venable and Levin (1985) tested this response further and found that germination of ray seeds was negatively correlated with burial depth, and as such they are an important part of the seed bank. In seed bank studies, only ray seeds were found in the soil (Palmer 1982; Venable et al. 1987; Tanowitz et al. 1987). This light response raises questions about the representativeness of the observed germination of ray seeds in our laboratory germination study. Since the germinations were conducted in the dark, except when checked for germination, this could have affected germination

TABLE 3. RESULTS OF GERMINATION BY SEED AGE LINEAR REGRESSION OF LABORATORY GERMINATION EXPERIMENT. ** Regression is significant at P < 0.017.

Species	Morph	Regression equation	R^2	n	F	P
B. plumosa	disc	% germination = −0.33 seed age + 0.779**	0.55	25	32.7	<0.0001
B. plumosa	ray	% germination = 0.017 seed age + 0.002**	0.29	25	11.7	0.0021
B. laxa	disc	% germination = 0.077 seed age − 0.099**	0.42	16	13.3	0.0022
B. laxa	ray	% germination = (9.25×10^{-18}) seed age + 0.03	0.06	16	0	1

rates. We may have seen a higher percentage of germination from ray seeds had they been kept in a lighted environment.

Temperature also has an influence on ray seed germination in some species. Baskin and Baskin (1976) found that ray seed after-ripening and subsequent germination in *H. s.* var. *subaxillaris* was inhibited at low temperatures and promoted at high temperatures. They interpreted this response in the context of natural environmental conditions for the winter annual, concluding that ray seeds over-winter for at least one season following dispersal and possibly more, while disc seeds germinate during the first autumn following dispersal. Since our store of seeds used for the laboratory germination study were kept at room temperature, this may also have affected ray seed germination.

Seed production and survivorship. Blepharizonia laxa consistently produced more disc seeds than ray seeds. *Blepharizonia plumosa* derived from disc seeds produced more ray seeds than disc seeds, and ray-seed derived plants produced no seeds at all. As presented in Fig. 5, the majority of the mature seeds produced by *B. plumosa* are ray seeds, which, as discussed above, are less likely to germinate, and if they do germinate, are less likely to produce seeds. Although most of the seeds produced by the *B. laxa* originated from ray-derived plants, this was due to the death of several of the disc-derived *B. laxa* plants just prior to seed maturation. Had this mortality not occurred, the disc-derived *B. laxa* may also have outpaced disc-derived *B. plumosa* plants in seed production since the biomass of the disc-derived *B. laxa* plants was comparable to that of the ray-derived *B. laxa* plants. Also, the disc-derived *B. laxa* plants that died were very large and contained a large number of inflorescences. Although there does not appear to be a survivorship difference between the disc-derived plants of the two species, the survivorship of ray-derived *B. plumosa* plants was lower than that of *B. laxa* ray-derived plants. This difference in survivorship was mirrored by the differences in biomass between the two species.

Interspecific differences and evolutionary consequences. The main differences between the two species appear to be related to the production of dimorphic seeds and the correlation of dimorphism to germination. *Blepharizonia laxa* produces more disc seeds than ray seeds, while this ratio is inverted, and is more extreme, for *B. plumosa*. Germination rates differed between disc and ray seeds in *B. plumosa* but did not differ for *B. laxa*. *Blepharizonia laxa* disc seed germination increased with age, while *B. plumosa* disc seed germination decreased with age. *Blepharizonia plumosa* ray seed germination increased with age, while *B. laxa* ray seed germination remained the same regardless of age.

The morphology of disc seeds is different between the two species: disc seeds have only a small pappus in *B. laxa,* but have a large pappus in *B. plumosa,* but the ray seed morphology between the two species is more similar (small to nonexistent pappus). The function of seed dimorphism in the ecology of each species may be different. Pappus presence is usually associated with greater dispersal ability and hence differences in pappus presence may be related to differences in seed bank dynamics (Palmer 1982; Venable et al. 1987; Tanowitz et al. 1987) and bet-hedging strategies (Westoby 1981) between the two species.

The evolutionary value of the poor ray seed performance of *B. plumosa* in the field is a puzzle. A question important to many species in Asteraceae is why would a species put so many resources into production of seeds that do not germinate? One explanation could be that ray seeds form the primary seed bank supply, buffering the population for future poor production years. Our study did not fully determine what factors affect ray seed dormancy. As discussed above, light and temperature may play an important role in ray seed germination, and this should be evaluated in future studies.

Areas at Site 300 where *B. plumosa* occurs are subject to routine annual burning. Fire may aid the survival of *B. plumosa* by promoting the growth of native bunch grasses, which may provide a more favorable habitat. However, as we observed, fire also caused direct mortality of seedlings found in the path of a controlled burn. Populations that are routinely burned may therefore depend upon ray seeds, assuming they are a significant part of the seed bank. Reasons for the difference in the prevalence of the two species at Site 300 still elude us. *Blepharizonia laxa* seed exhibits lower germination percentages than *B. plumosa* seed. However, *B. laxa* plants produce more seed for compensation. It is likely that fire plays a differential role in facilitating germination between the two species.

Population differentiation and mitigation. Little differentiation was found between populations of *B. plumosa*. The fact that some differences were seen in the reciprocal transplant experiment germination percentages indicates that some populations may respond better to mitigation than others. Additional experiments with larger sample sizes should be performed prior to any mitigation work. However, we do have a good foundation upon which future experiments relating to population relocation can be performed. The high disc seed germination rates observed for each parent population at each transplant site indicate that seeds from multiple, local populations could be used for this new population. Since the low ray seed germination rate was not mitigated by transplant site/soil type, and not much is known about factors affecting dormancy, ray seeds would not be used as a seed source for this population. At present, it is unknown whether successful long-term establishment of new populations

would be possible. This can only be determined through long-term monitoring and experimental manipulation of both new and existing populations.

Future Studies

Continued monitoring of populations of *B. plumosa* and *B. laxa* within controlled burn areas and comparing them to populations that are not routinely burned will help elucidate the impacts of fire on these populations and the reasons for the different distributions of these two species at Site 300. Factors affecting ray seed dormancy in *B. plumosa* and the role of ray seeds in populations of this species deserve further examination in order to develop the most informed management strategy for this rare plant.

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RECRUITMENT OF *FRAXINUS PENNSYLVANICA* (OLEACEAE) IN EASTERN MONTANA WOODLANDS

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Abstract

Fraxinus pennsylvanica Marsh. (Oleaceae) woodlands are an important habitat for conservation of biological diversity on the Northern Great Plains. Many *F. pennsylvanica* woodlands appear to lack tree regeneration; however, little is known about the mode of recruitment in these stands. I sampled species composition, seedling density and the extent of vegetative recruitment of *F. pennsylvanica* for 17 stands in east-central Montana. Stand age distributions indicate that recruitment during the past 50 years has been greatly reduced compared to the previous 50 years. Detrended Correspondence Analysis identified a strong gradient in species composition positively associated with canopy cover of tall shrubs and mean annual precipitation and negatively associated with exotic grasses. Seedling recruitment of *F. pennsylvanica* was more common in stands with high DCA scores. The frequency of multi-stem tress indicated that at least 30% of *F. pennsylvanica* trees arose vegetatively. Rejuvenating sparse *F. pennsylvanica* woodlands should include both vegetative and seedling tree recruitment. Burning and/or cutting old, diseased trees with sparse canopies could create more vigorous stands once the sprouts have matured. Shadier habitat of such stands may encourage seedling recruitment by reducing the vigor of sod grasses.

Fraxinus pennsylvanica Marsh woodlands are found along small-order drainages and on moist, cool slopes throughout much of the eastern third of Montana as well as most of the Northern Great Plains. Although *F. pennsylvanica* woodlands comprise only a small proportion of this prairie landscape, their aesthetic, economic and biological values are large compared to their aerial extent (Noble and Winokur 1984). Many species of plants and animals occur only in habitat provided by *F. pennsylvanica* woodlands. For example, Faanes (1984) recorded 47 species of breeding birds in western North Dakota woodlands, 22 of which were neotropical migrants. Of the 81 species of birds observed in *F. pennsylvanica* woodlands by Rumble and Gobeille (1998), 65 require woodland habitat. Lesica (1989) lists several vascular plant species occurring in eastern Montana only or primarily in *F. pennsylvanica* woodlands.

Unfortunately, evidence from throughout the Northern Great Plains suggests that tree recruitment has declined in many *F. pennsylvanica* woodlands (Boldt et al. 1978; Lesica 1989). Woodlands with dense, stratified canopies and undergrowth dominated by native shrubs, graminoids, and forbs are being replaced by open canopy communities with few tall shrubs in the understory and a ground layer dominated by introduced sod-forming grasses (Hansen and Hoffman 1988). Many native animals decline as woodlands become more open. Bird density and diversity was lower in these open-canopy stands in northwestern South Dakota (Hodorff et al. 1988; Rumble and Gobeille 1998). Deer mice (*Peromyscus maniculatus*), white-footed mice (*Peromyscus leucopus*) and woodrats (*Neotoma cinerea*) occurred more commonly in closed-canopy stands, while no mammalian species was more common in the open stands (Hodorff et al. 1988).

It is imperative to maintain existing closed canopy *F. pennsylvanica* woodlands and restore open stands in order to maintain biological diversity of the Northern Great Plains. Management and restoration of these woodlands hinges on understanding tree recruitment. *Fraxinus pennsylvanica* reproduces from seed and by vegetative sprouting from the tree base (Hansen et al. 1984; Uresk and Boldt 1986; Lesica 1989; Sieg and Wright 1996). However, the past and present importance of these two modes of recruitment in native woodlands is not known. In this study I measured current levels of vegetative and seedling recruitment in relation to current stand condition to help determine what environments are conducive to recruitment. I also obtained age-class distributions from increment core data to gain insight into past recruitment regimes. Results are used to develop restoration and management strategies.

Study Sites

I conducted my study at six sites in Custer, Dawson, Fallon, McCone, Prairie and Wibaux counties in east-central Montana (Fig. 1). Elevations of the study sites range from 745 m at Fort Peck to 1005 m at Cedar Creek. Soils are derived from soft sandstones, siltstones and claystones of the late Cretaceous Fort Union Formation (Veseth and Montagne 1980). Climate of the study area is semi-arid and continental. Mean annual precipitation ranged from 29 cm at Fort Peck to 41 cm between Baker and Wibaux (USDA-SCS 1981). Mean January minimum and July maximum temperatures at Terry in the center of the study area were $-18°$ and $31°C$ respectively (NOAA 1982). Mean annual precipitation for the study areas was derived from a map
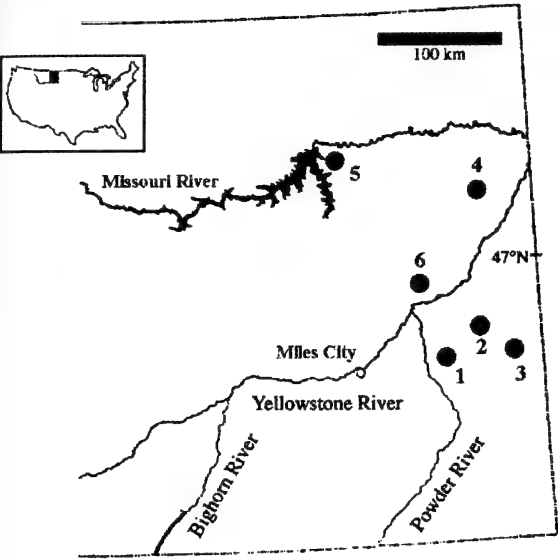
FIG. 1. Location of six study sites in east-central Montana: (1) Rattlesnake Butte, (2) Cabin Creek, (3) Wibaux, (4) Bible Camp, (5) Fort Peck, (6) Cedar Creek.

of precipitation isohyetal lines for Montana for the period 1941-1970 (USDA-SCS 1981).

Upland vegetation of the study area is steppe dominated by *Artemisia tridentata* ssp. *wyomingensis* Beetle and Young and perennial grasses including *Stipa comata* Trin. and Rupr., *Agropyron smithii* Rydb. and *Bouteloua gracilis* (H. B. K.) Griffiths Woodland vegetation dominated by *F. pennsylvanica* occurs in narrow bottomlands along ephemeral drainageways dissecting the uplands. These "woody draws" often occur at the head of drainage basins but may be found along channels farther downstream as well.

SPECIES DESCRIPTION

Fraxinus pennsylvanica is a small, dioecious, deciduous tree to 20 m tall and 50 cm in diameter in Montana. It is shallow rooted and common along streams and in floodplains and other bottomland habitats from Nova Scotia to Alberta south to Texas and Florida (Great Plains Flora Association 1986; Farrar 1995). *Fraxinus pennsylvanica* is reported to have a short-lived seed bank (Farrar 1995). Seedlings grow equally well in sun or shade (Borger and Kozlowski 1972). Wood is hard and was extensively cut for firewood, especially in the prairie states (Peattie 1953). Maximum age is thought to be ca. 100 years (Farrar 1995) Montana plants are sometimes considered to be var. *lanceolata* or var. *subintegerrimus,* but these varieties are now considered of little taxonomic value (Great Plains Flora Association 1986).

METHODS

Field methods. I sampled 17 stands among the six study sites. Stands were stratified by county and selected randomly from a list of stands managed by the USDI Bureau of Land Management. Only stands more than 2 ha in extent with *Fraxinus pennsylvanica* canopy cover reported to be at least 40% were included in the original pool of stands.

After thorough reconnaissance, I subjectively located a 50 × 20 m sample plot to represent each stand. I estimated total tree canopy cover with a spherical densiometer at 12.5 and 37.5 m along the center line of each plot. I also recorded ocular estimates of canopy cover of all woody plants and all herbaceous plants with cover of 1% or more. Vascular plant nomenclature follows Great Plains Flora Association (1986).

In each plot I recorded the total number of trees equal to or greater than 2 m high into five 10-cm size classes by species. I tallied all trees in the sample plot into size classes and noted the presence of multiple stems and trunk sprouts (shoots arising vegetatively from the tree base) for all trees. Density of tree seedlings (stems <2 m tall and ≤10 yrs old not arising from an older plant) was estimated from four 20 m^2 or 50 m^2 circular subplots equidistant along the macroplot center line. Larger subplots were used when seedling density was low.

I obtained the age, diameter and height of one randomly chosen sample tree of each species in each size class in each quarter-section of each plot. I estimated the height of sample trees to the nearest 0.5 m with a 3-m gauging pole. Diameter was measured to the nearest 1 cm with a tape. Age was obtained from increment cores taken at 0.5 m above ground level. The number of annual rings was counted using a 10–20× microscope with crossdating to help assure accuracy (Stokes and Smiley 1996). This method could underestimate the true age if tree stems were less than 0.5 m for one or more years. Several sample trees had rotten centers, and age could not be determined. Diameter of multiple-stem trees was calculated as the diameter of a single-stem tree of equivalent basal area.

Data analysis. Stand-level basal area of tree species was estimated by assigning the midpoint of each diameter size class to all trees in that class. I used the coefficient of variation (cv, standard deviation/mean) as a measure of how evenly distributed tree ages were within stands.

I ordinated common species and stands using Detrended Correspondence Analysis (DCA; Gauch 1982; Rasmus 2000) to elucidate environmental gradients important to recruitment. Canopy cover estimates of all species present in at least five stands were used as input (McCune and Mefford 1997).

I used regression analysis to test the significance of associations between precipitation and vegetation (DCA score) and the proportions of trees with

TABLE 1. FREQUENCY OF OCCURRENCE, MEAN PERCENT CANOPY COVER AND DCA AXIS 1 SCORES FOR COMMON (FREQUENCY >25%) SPECIES IN 17 SAMPLE STANDS.

	Frequency	% cover	DCA score
Trees			
Acer negundo	7	2	233
Fraxinus pennsylvanica	17	37	120
Shrubs			
Amelanchier alnifolia	7	1	211
Prunus americana	6	1	226
Prunus virginiana	15	16	243
Ribes setosum	12	<1	20
Rosa woodsii	10	1	−18
Symphoricarpos occidentalis	14	12	26
Toxicodendron rydbergii	6	1	138
Graminoids			
Agropyron repens	5	3	81
Bromus inermis	7	9	−91
Bromus japonicus	6	8	24
Carex sprengelii	5	14	323
Poa pratensis	15	26	−14
Forbs			
Achillea millefolium	5	<1	−26
Arctium minus	6	1	269
Cystopteris fragilis	6	<1	288
Disporum trachycarpum	6	<1	169
Galium aparine	11	1	289
Galium boreale	6	<1	161
Hackelia deflexa	6	<1	162
Monarda fistulosa	5	<1	27
Ranunculus abortivus	6	<1	273
Smilacina stellata	10	2	158
Smilax herbacea	7	<1	120
Taraxacum officinale	8	4	12
Thalictrum spp.	10	<1	252
Viola canadensis	5	<1	69

trunk sprouts and multiple stems and between seedling density and precipitation, vegetation and cv of tree age. I used Analysis of Variance (ANOVA) to test the effect of the presence of multiple stems and trunk sprouts on tree age and size. Mixed models included site and an interaction term as factors. The main effect was tested against the interaction term when the latter was significant ($P \leq 0.10$).

RESULTS

Stand descriptions. *Fraxinus pennsylvanica* woodlands had total tree canopy cover of 18% to 73% with a mean of 45%. *Fraxinus pennsylvanica* was the dominant tree in all stands. Basal area ranged from 5.6 m²/ha to 37.5 m²/ha with a mean of 14.9 m²/ha, and mean canopy cover was 37% (SE = 4%). *Acer negundo* L. (boxelder) occurred in six stands with a mean basal area of 2.2 m²/ha and mean canopy cover of 7%. *Ulmus americana* L. (American elm) occurred in three of the four easternmost stands with a mean basal area of 5.7 m²/ha and a mean canopy cover of 22%.

Fraxinus pennsylvanica trees were 2.0 to 14.5 m

tall with a mean of 7.0 m (N = 204, SE = 0.2 m) and basal diameters of 2.5 to 65 cm with a mean of 23 cm (n = 227, SE = 1 cm). *Ulmus americana* occurred in three sample stands at the Wibaux and Bible Camp sites. Diameter of *U. americana* ranged from 7 cm to 68 cm with a mean of 25 cm (N = 20, SE = 3 cm). Height varied from 5 m to 14 m with a mean of 9 m (SE = 0.5 m). I sampled only 10 *Acer negundo* trees, all of which were at the Cabin Creek and Wibaux sites. Diameter ranged from 20 cm to 50 cm with a mean of 30 cm (n = 10, SE = 3 cm). Height ranged from 6 m to 13 m with a mean of 8 m (n = 8, SE = 1 m).

Detrended Correspondence Analysis (DCA) identified one strong gradient; axis 1 accounted for 64% of the variation in species composition. Species with low scores for DCA axis 1 included introduced rhizomatous grasses, *Bromus inermis* Leyss. and *Poa pratensis* L. as well as the low shrubs, *Symphoricarpos occidentalis* Hook. and *Rosa woodsii* Lindl. The weedy forbs, *Achillea millefolium* L. and *Taraxacum offiicinale* Weber also had low scores (Table 1). Species at the high end
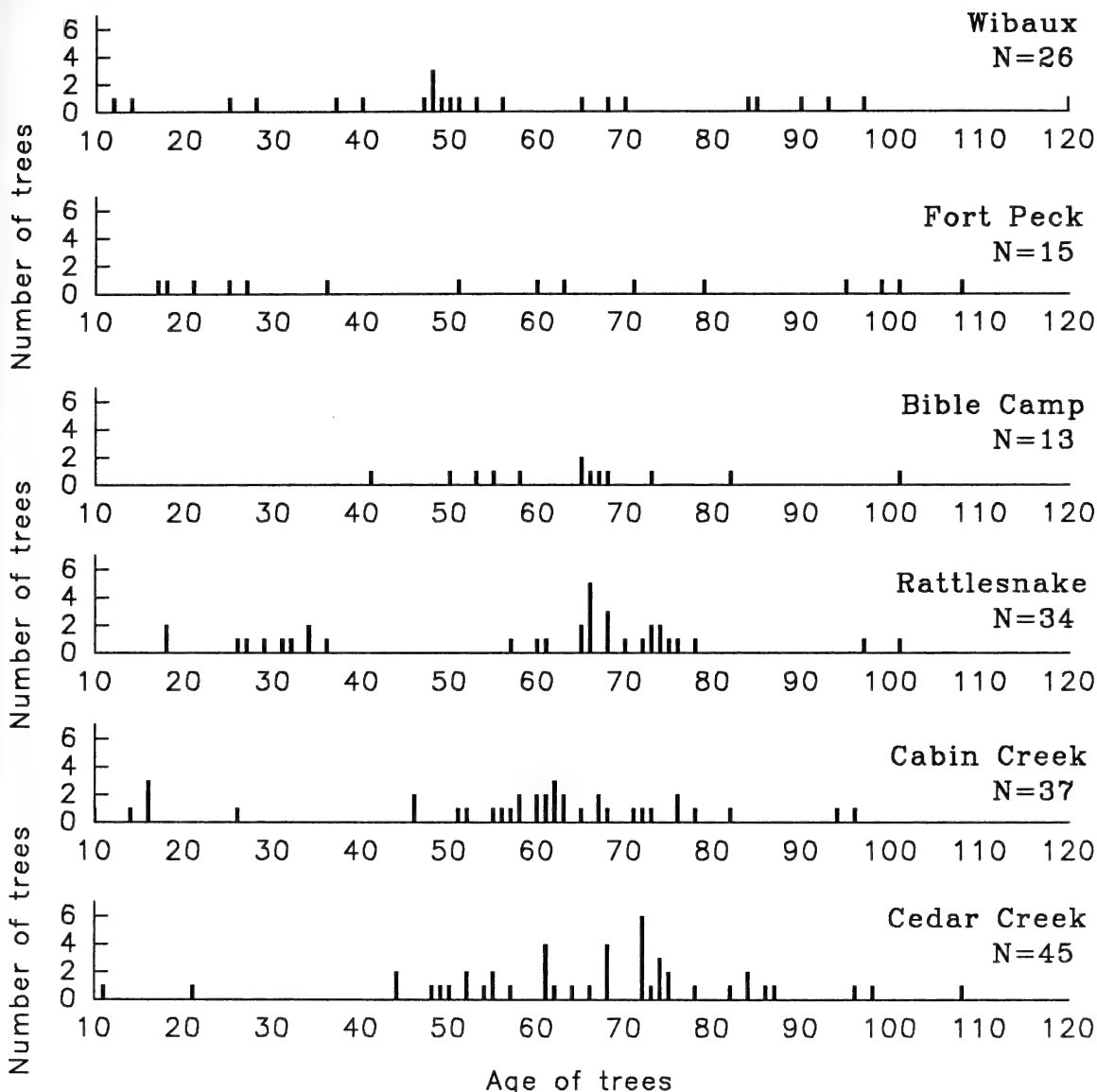
FIG. 2.   Age distribution of *Fraxinus pennsylvanica* at six study sites in east-central Montana.

of DCA axis 1 include the tall shrubs *Prunus virginiana* L., *P. americana* Marsh and *Amelanchier alnifolia* Nutt. The highest score was assigned to *Carex sprengelii* Dewey, a native graminoid. Common forest species, *Galium aparine* L., *Cystopteris fragilis* (L.) Bernh., *Ranunculus abortivus* L. and *Thalictrum* spp. and the mesic-loving exotic, *Arctium minus* Bernh., also had high scores (Table 1). Stands with high DCA scores had higher mean annual precipitation ($R^2 = 0.26$, $P = 0.036$). Canopy cover of tall *Prunus* spp. ranged from 0% to 65% and was negatively correlated with the canopy cover of introduced rhizomatous grasses which ranged from 0% to 86% ($r = 0.58$, $P = 0.016$). Higher DCA scores were associated with lower canopy cover of exotic species ($R^2 = 0.80$, $P < 0.001$), and

a model with both precipitation and cover of exotics explained 86% of the variation in vegetation ($P < 0.001$).

Recruitment. *Fraxinus pennsylvanica*, *Ulmus americana* and *Acer negundo* all reproduced both vegetatively and from seed in study plots. However, sample sizes were large only for *F. pennsylvanica*, so results and discussion will be limited to this species.

Age distributions of *F. pennsylvanica* trees indicate that most stands were not even-aged, and recruitment was sporadic (Fig. 2). A disproportionately large number of *F. pennsylvanica* trees in sample stands were 60–75 years old. Over all sites, 39% of the *F. pennsylvanica* trees regenerated in

the 15-year period of 1926–1940. Only 27% (n = 173) of the *F. pennsylvanica* trees sampled were 50 years or younger, and only 3% were 100 years or older.

An average of 33% of *F. pennsylvanica* trees in study stands had live sprouts at their base, and 30% had more than one bole, indicating that they arose as basal trunk sprouts. Sprouting trees were larger than trees without sprouts with a mean diameter of 24 cm (SE = 1 cm) compared to 20 cm (SE = 1 cm; $F_{1,206}$ = 8.7, P = 0.003). However, the mean age of sprouting and non-sprouting trees did not differ (P = 0.296). Multi-stem trees averaged 64 years (SE = 3 yrs) compared to 58 years (SE = 2 yrs) for single-stem trees ($F_{1,158}$ = 4.0, P = 0.05). The abundance of multi-stem and sprouting trees was not associated with vegetation (P > 0.62).

Fraxinus pennsylvanica seedlings were uncommon in most stands. Mean number of seedlings per 100 m^2 was 10 (SE = 5). Nine of 17 stands (53%) had one or fewer seedlings per 100 m^2, and seedlings were entirely absent from sample plots in five stands. There was no association between mean annual precipitation and seedling density (R^2 = 0.02, P = 0.58). However, higher seedling density was associated with more mesic vegetation (high DCA axis 1 scores; R^2 = 0.23, P = 0.05), and this association was due more to a positive correlation with canopy cover of *Prunus* spp. (r = 0.71) than a negative correlation with exotic rhizomatous grasses (r = −0.39). Stands in which tree ages were more evenly distributed (as measured by the coefficient of variation for age) tended to have more seedlings (R^2 = 0.22, P = 0.06).

DISCUSSION

The age structure of *Fraxinus pennsylvanica* stands indicates that recruitment in the second half of the past century has been low relative to the first half. Nearly 75% of *F. pennsylvanica* trees in sample stands were 50 years or older. *Fraxinus pennsylvanica* stems rarely persist more than 100 years on the Northern Great Plains (Butler and Goetz 1984; Girard 1985; Hansen et al. 1984; Hansen and Hoffman 1988; Farrar 1995; Sieg 1991) so density of *F. pennsylvanica* stems will decline by 50% over the next 50 years under current levels of recruitment.

Sprouting from the base of the trunk is an important mode of reproduction in *F. pennsylvanica*. A minimum of 30% of the trees in our sample stands arose as basal trunk sprouts, and vegetative reproduction occurred regardless of differences in associated vegetation. Although sprouting ability may be a function of tree size, younger trees were not more likely to sprout than older trees. More than 90% of *F. pennsylvanica* sprouted after being cut in an experiment in North Dakota (Uresk and Boldt 1986), although it is not known what proportion of these survived to become trees.

The large pulse of *F. pennsylvanica* recruitment that occurred between 1926 and 1940 may well have been due to trunk sprouting. Many trees were cut down by the large influx of homesteaders during the years of 1900–1918 (Malone and Roeder 1976). Starting around 1920 a decline in farm prices and a series of severe droughts led to a rapid reduction in the rural population (Malone and Roeder 1976) and a concomitant lessening of woodcutting and livestock numbers (Lee and Williams 1964), undoubtedly leading to lower woodcutting and grazing pressure. Interviews with long-time residents indicate that fire was not a significant factor (Lesica and Atthowe 2001). However, *F. pennsylvanica* may have responded directly to the drought conditions of the mid-1920's and 1930's by dying back to the ground and resprouting (Albertson and Weaver 1945). It is conceivable that whole stands rejuvenated during this time by trunk sprouting alone. However, it seems unlikely that *F. pennsylvanica* woodlands can persist over the long term relying solely on vegetative reproduction to provide a tree canopy.

Fraxinus pennsylvanica stands with higher densities of tree seedlings tended to have a greater array of tree ages, suggesting that steady recruitment from seed produced more uneven age structures than sporadic vegetative recruitment following drought, woodcutting or fire. However, *F. pennsylvanica* seedlings were uncommon in most stands and entirely absent from five of 17 sample plots. Lack of recruitment from seed during the past 50 years or longer has probably contributed to the skewed age distributions of most sample stands.

Fraxinus pennsylvanica woodland vegetation occupied a gradient from stands dominated by sun-loving, exotic grasses, grassland forbs and low shrubs to those with more closed understories dominated by *Prunus virginiana, P. americana, Amelanchier alnifolia, Carex sprengelii* and shade-loving forbs. Several other researchers have observed the same gradient in Montana and the Dakotas (Butler and Goetz 1984; Girard et al. 1987; Hansen and Hoffman 1988; Hodorff et al. 1988; Lesica 1989; Vorhees and Uresk 1992). Recruitment of tree seedlings was higher beneath more closed understories. The gradient defined by DCA axis 1 was associated with increasing mean annual precipitation, and decreasing canopy cover of exotic species. Abundance of exotics is frequently associated with level of disturbance, especially by livestock (Parker et al. 1993; Kotanen et al. 1998; Smith and Knapp 1999). Woodlands receiving more precipitation may be more resilient to grazing disturbance (Fahnestock and Detling 1999). Assuming that canopy cover of exotic species is a surrogate for disturbance, these results suggest that drought stress and overgrazing disturbance work in concert to favor stands with a more xeric, meadow-like understory, less conducive to tree seedling recruitment.

The association between density of seedlings and

more mesic, less disturbed stands characterized by a high canopy cover of *Prunus* spp. and lower abundance of rhizomatous grasses suggests that recruitment of *F. pennsylvanica* from seed may depend on facilitation by a tall shrub understory. Reduced vigor of sod grasses associated with shading by a healthy shrub layer would likely mean more safe sites for tree seedlings (Albertson and Weaver 1945; Petranka and McPherson 1979; Van Auken and Bush 1997). In addition, *F. pennsylvanica* seedlings are very shade-tolerant (Borger and Kozlowski 1972), so interference from the *P. virginiana* canopy may be minimal. Tree seedlings may also experience a more humid environment and less herbivory under a shrub canopy (Callaway 1992, Werner and Harbeck 1982). The relationship between *P. virginiana* and tree recruitment could be pivotal to succession from a meadow/low shrub community to *F. pennsylvanica* woodland. Facilitation of *F. pennsylvanica* recruitment by *Prunus* species in these woodlands is plausible but requires experimental study for verification.

Recruitment of trees both vegetatively and from seed has been important in *F. pennsylvanica* woodland dynamics in the past. Rejuvenating open green ash woodlands is likely best accomplished by encouraging tree recruitment through both of these modes. Uresk and Boldt (1986) rejuvenated western North Dakota *F. pennsylvanica* woodlands by cutting decadent trees. Nearly all the trees sprouted after cutting. Prescribed fire may also be useful in encouraging vegetative recruitment of trees; low-intensity experimental burns induced sprouting of *F. pennsylvanica* in northwestern South Dakota (Sieg and Wright 1996). Burning and/or cutting old, diseased trees with sparse canopies could eventually create stands with greater canopy leaf area once the sprouts have matured. Tall shrub densities may also increase in stands exposed to fire (Zimmerman 1981). Shadier habitat of stands rejuvenated by cutting or fire should encourage seedling recruitment by reducing the vigor of rhizomatous sod grasses. However, fire could increase the abundance of exotic grasses in the short term by decreasing shade and increasing nutrient availability (Blair 1997).

These proposed restoration methods need to be tested in controlled experiments with livestock grazing excluded. Cattle will use woodland habitat heavily during the growing season (Boldt et al. 1978), resulting in lower canopy cover of tall shrubs (Butler and Goetz 1984; Hansen and Hoffman 1988). Tree sprouts grew taller, and survival of planted *F. pennsylvanica, Prunus virginiana* and *P. americana* was higher in ungrazed stands compared to stands grazed by cattle (Uresk and Boldt 1986). Further studies on the effects of tall shrubs and fire on seedling recruitment are needed.

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HARMONIA GUGGOLZIORUM (COMPOSITAE-MADIINAE), A NEW TARWEED FROM ULTRAMAFICS OF SOUTHERN MENDOCINO COUNTY, CALIFORNIA

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Abstract

Harmonia guggolziorum is a new tarweed from ultramafic (serpentine) soils of southern Mendocino County, California. Unlike other species of *Harmonia, H. guggolziorum* combines the following morphological characteristics: primary stems usually longer than branches of the subumbelliform capitulescences, leaves unevenly distributed but not densely congested, heads erect in bud and fruit, phyllaries irregularly hirsute, disc florets bisexual, ray cypselae weakly arcuate, ray pappi present, and disc pappi of linear, fimbriate scales 0.6–0.8 mm long. Based on molecular phylogenetic data, I suggest that *H. guggolziorum* is the only known representative of a lineage that predates diversification of the other serpentine endemic species of *Harmonia* (i.e., *H. doris-nilesiae, H. hallii,* and *H. stebbinsii*). The apparent phylogenetic relationships and geographic location of *H. guggolziorum* lead me to hypothesize that *Harmonia* originated in the southern North Coast Ranges and has undergone more extensive diversification on ultramafics than previously suspected for the genus or any other lineage in Madiinae.

California's exceptionally rich serpentine flora is especially well represented in the northwestern part of the state (Kruckeberg 1984, Harrison et al. 2000), where botanical exploration has continued to reveal previously unknown ultramafic endemics. In the tarweed genus *Harmonia* B. G. Baldwin [=*Madia* Molina sensu Keck (1959) pro parte (i.e., the yellow-anthered, pappose annuals, with $2n = 9$ II); see Baldwin (1999)], two ultramafic endemics (*H. doris-nilesiae* and *H. stebbinsii*) have been described from the North Coast Ranges of California since 1980 (Nelson and Nelson 1980, 1985). Herein, I describe yet another species of *Harmonia* from the North Coast Ranges.

Harmonia guggolziorum B. G. Baldwin, sp. nov. (Fig. 1)—TYPE: USA, California, Mendocino Co., on serpentine on the north side of Feliz Creek Road (County Road 109), 2.1 miles west of Hopland (T13N, R12W, S23, NW1/4 of NE1/4), ca. 150–200 plants associated with *Platystemon californicus, Gilia capitata,* and *Cryptantha clevelandii*, 164 m, 30 April 2000, *Jack and Betty Guggolz 1635* (holotype, JEPS; isotype, CAS).

Ab species ceteris Harmoniae characteribus combinatis differt caulibus primariis plerumque ramis subumbelliformium capitulescentiarum longioribus; foliis distributis impariter, non dense congestis, plerumque proximalibus in caulibus primariis et ad basibus capitulescentiarum; capitulis plerumque erectis ante, per, et post anthesin; phyllariis irregulariter et saepe sparsim hirsutis cum pilis prope margines mollibus saepe implicitis; flosculis discorum bisexualibus; cypselis radiorum leniter arcuatis;

squamis papporum radiorum fimbriatis, ca. 0.5 mm longis; squamis papporum discorum linearibus fimbriatis ca. 0.6–0.8 mm longis.

Annual herbs. Stems erect, branched mostly in distal half, slender, mostly reddish-purple, to 3 dm high, sparsely to densely hirsute proximally, densely stipitate-glandular distally, the glands dark-purplish (or yellowish). *Leaves* opposite proximally, alternate distally, sessile, mostly cauline, unevenly distributed, mostly proximal on primary stems and at bases of capitulescence branches (otherwise sparse or absent), ascending or usually widely spreading, often with reflexed apices; blades linear to filiform, 5–50 mm long (mostly 20–25 mm long on primary stems), 1–3 mm wide, entire or sparsely and shallowly toothed, slightly revolute, hirsute, eglandular or (mostly in capitulescence) stipitate-glandular (especially near apices), the glands dark-purplish (or yellowish). *Capitulescences* subumbelliform, branches often 5–7 cm long (max. 15 cm long) and overtopping the nearly sessile head of the primary stem. *Peduncles* 2–12 mm long, stipitate-glandular, the glands dark-purplish (or yellowish). *Heads* usually erect in bud, anthesis, and fruit. *Involucres* obovoid, ca. 3–4 mm diam. (4–5 mm diam. in pressed specimens). *Phyllaries* (3–) 5 (–6) (1 per ray floret), uniseriate, herbaceous, linear, 4–5 mm long, each completely enveloping a ray ovary, the free apices purplish, erect or spreading, flat or involute, <1/5 the length of enfolded basal portion of phyllaries; abaxial faces irregularly and often sparsely hirsute with broadly arching or somewhat appressed hairs, often with soft, matted hairs near margins, ciliate, irregularly stipitate-glandular, the glands dark-purplish (or yellowish). *Ray florets*
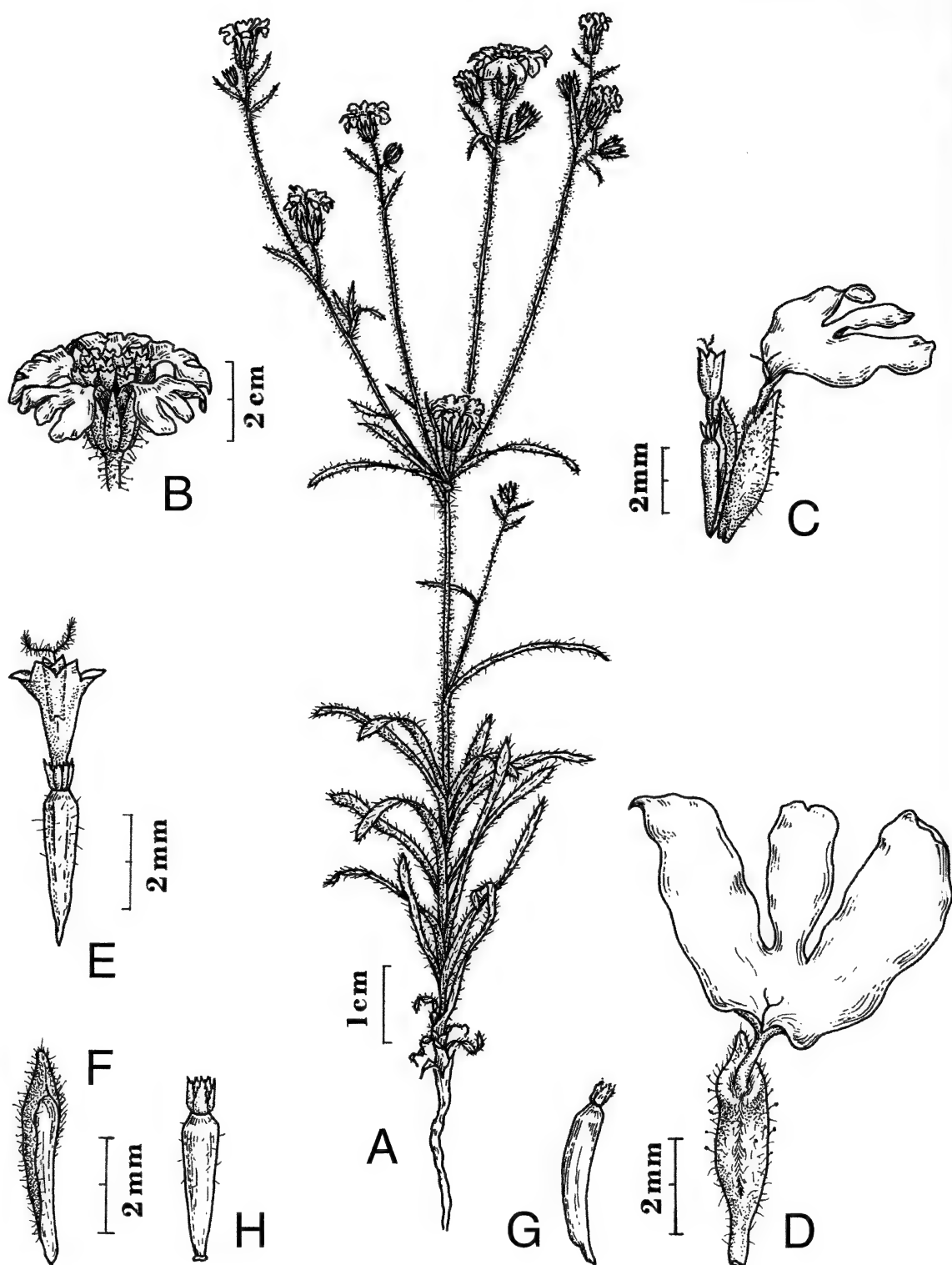
FIG. 1. *Harmonia guggolziorum.* (A) habit; (B) head; (C) phyllary, ray floret, palea, and disc floret (right to left); (D) adaxial view of ray floret and associated phyllary; (E) disc floret; (F) palea; (G) ray cypsela and pappus; (H) disc cypsela and pappus.
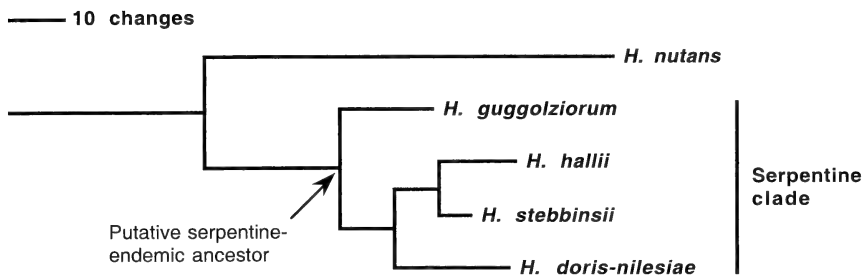
FIG. 2.   Relationships in *Harmonia* based on 18S/26S nuclear ribosomal DNA sequences of the external and internal transcribed spacer regions (Baldwin, unpublished). The tree is rooted with sequences from the other diploid members of the "Madia" lineage (Baldwin 1996).

(3–) 5 (–6), pistillate, corollas bright yellow, tubes ca. 1.5 mm long, sparsely hirtellous, laminae broadly overlapping in head, flabelliform, 4–5 mm long, 5–7 mm wide, 3-lobed to ca. half length, glabrous. *Disc florets* 8–13, bisexual, corollas bright yellow, 2–3.5 mm long, tubes much shorter than the narrowly funnelform throats, lobes 5, glabrous abaxially, densely bristly adaxially. *Anthers* yellow. *Style branches* acuminate, hispidulous. *Receptacles* flat, glabrous. *Paleae* not persistent, ca. 8, in one peripheral series, linear, 4–5 mm long, herbaceous near apices or throughout, sometimes chartaceous proximally (especially along margins), flat or with margins partially enveloping a disc ovary, sparsely hirsute and densely ciliate near apices, sparsely stipitate-glandular near apices, the glands dark-purplish (or yellowish), the margins of adjacent bracts

free or weakly fused proximally. *Ray cypselae* black, slightly laterally compressed, abaxially rounded, adaxially angled, clavate, weakly arcuate, ca. 3–3.5 mm long, glabrous, beakless. *Ray pappi* of ca. 10–12 stramineous, linear, fimbriate scales ca. 0.5 mm long. *Disc cypselae* black, ±terete to clavate, straight or weakly arcuate, ca. 3–3.5 mm long, with antrorse hairs. *Disc pappi* of ca. 9–11, stramineous or purplish, linear, ±flat (not crisped), fimbriate scales, 0.6–0.8 mm long. *Chromosome number* $2n = 9$ II [reported here from *B. G. Baldwin 1140* (JEPS)].

Paratype. USA, California, Mendocino County, on serpentine hillside at junction of Feliz Creek Road (County Road 109) and County Road 110, west of Hopland, 8 May 2001, *B. G. Baldwin 1140* (JEPS).

KEY TO SPECIES OF *HARMONIA*

1. Heads usually reflexed in bud and fruit; ray pappi 0; disc pappus elements lance-attenuate, fimbrillate, 2–3.7 mm long . . . . *H. nutans* (Greene) B. G. Baldwin
1′ Heads usually erect in bud and fruit; ray pappi present (often rudimentary); disc pappus elements subulate, linear, oblong, or quadrate, fimbriate or pulmose, 0.2–3.5 mm long.
2. Leaves ± evenly distributed along stems; ray cypselae gibbous (bowed out abaxially), distinctly beaked (beaks <1 mm long); disc florets functionally staminate . . . . *H. doris-nilesiae* (T. W. Nelson & J. P. Nelson) B. G. Baldwin
2′ Leaves unevenly distributed, mostly restricted to proximal stems and bases of subumbelliform capitulescences; ray cypselae weakly arcuate, beakless; at least some disc florets bisexual.
3. Phyllaries pilose near margins; disc pappus elements subulate, 1.2–3.5 mm long, plumose . . . . *H. stebbinsii* (T. W. Nelson & J. P. Nelson) B. G. Baldwin
3′ Phyllaries with inconspicuous, soft, often matted hairs near margins; disc pappus elements linear, oblong, or quadrate, 0.2–0.8 mm long, fimbriate.
4. Primary stems usually shorter than branches of the subumbelliform capitulescences; distal leaves of primary stem densely congested; disc pappus elements oblong or quadrate, 0.2–0.5 mm long. . . . . *H. hallii* (D. D. Keck) B. G. Baldwin
4′ Primary stems usually longer than branches of the subumbelliform capitulescences; distal leaves of primary stem not densely congested; disc pappus elements linear, 0.6–0.8 mm long . . . . *H. guggolziorum* B. G. Baldwin

Relationships. Based on phylogenetic analyses of 18S/26S nuclear ribosomal DNA sequences of the external and internal transcribed spacers (Baldwin, unpublished), *H. guggolziorum* represents a basally divergent lineage in a monophyletic group comprising all serpentine endemics in *Harmonia* (Fig. 2). Origin of the lineage represented by *H. guggolziorum* apparently predates divergence of *H. doris-*

nilesiae, H. hallii, and *H. stebbinsii* from a common ancestor; *H. guggolziorum* is the sister group of the lineage corresponding to *H. doris-nilesiae, H. hallii,* and *H. stebbinsii.* Support for the hypothesis that *H. guggolziorum* represents an ancient, divergent lineage in *Harmonia* rather than a recent product of hybridization comes from unique character-states at eight rDNA nucleotide sites in *H. guggolziorum*

and from four rDNA mutations shared by the other three serpentine species of *Harmonia* but not by *H. guggolziorum, H. nutans,* or any other diploid species of the "Madia" lineage (i.e., diploid species of *Anisocarpus* Nutt., *Carlquistia* B. G. Baldwin, *Jensia* B. G. Baldwin, *Kyhosia* B. G. Baldwin, or *Madia* Molina; see Baldwin 1996, 1999).

Biogeographic and evolutionary history of Harmonia. Discovery of *H. guggolziorum* has allowed for refined perspectives on the history of edaphic endemism and overall pattern of diversification in *Harmonia.* Based on phylogenetic analyses of rDNA sequence data (Fig. 2, Baldwin unpublished), the four species of ultramafic endemics in *Harmonia* (*H. doris-nilesiae, H. guggolziorum, H. hallii,* and *H. stebbinsii*) represent a well-supported monophyletic group that is sister to *H. nutans,* an endemic of volcanic-ash exposures in Napa and Sonoma counties, California. In light of the phylogenetic data, I propose a simple hypothesis to explain patterns of edaphic endemism in *Harmonia*: divergence of the ultramafic and volcanic-ash lineages from a common ancestor preadapted (preapted) to "harsh" edaphic conditions, followed by extensive diversification on serpentines in the ultramafic lineage, that is, descent of *H. doris-nilesiae, H. guggolziorum, H. hallii,* and *H. stebbinsii* from a common, ultramafic-endemic ancestor. Lack of diversity in the volcanic-ash lineage may be attributable in part to the limited geographic distribution of volcanic exposures in northwestern California compared to the wide distribution of serpentine exposures in the region (Kruckeberg 1984; Fox et al. 1985).

Phylogeographic considerations lead me to suggest a general history for *Harmonia* of wide dispersal and allopatric diversification among edaphic "islands" (see Raven 1964; Kruckeberg 1991). *Harmonia guggolziorum* and *H. nutans,* represented by two lineages that diverge in succession at the base of the *Harmonia* rDNA tree (Fig. 2), and *H. hallii* are allopatric or parapatric taxa that are endemic or largely restricted to the southern North Coast Ranges (*H. nutans* extends south into the northern San Francisco Bay area). The two species of the northern North Coast Ranges and southern Klamath Ranges (*H. doris-nilesiae* and *H. stebbinsii*) are apically nested in the rDNA tree among the southern North Coast Range lineages and therefore are suggested to be products of dispersal from the south. Based on the rDNA tree topology, *H. doris-nilesiae* and *H. stebbinsii* are not sister species and may represent independent south-to-north dispersal events. Alternatively, the two species may have descended from the same northerly-dispersed ancestor, with *H. hallii* representing an instance of north-to-south dispersal. *Harmonia doris-nilesiae* and *H. stebbinsii* are highly divergent in morphology and molecular sequences and are to my knowledge the only taxa in *Harmonia* that provide an example of

sympatry [*V. Parker 757* (JEPS) and *V. Parker 759* (JEPS), at a site southwest of Dubakella Mountain, Trinity Co., California].

In summary, members of the ultramafic clade of *Harmonia* appear to be outstanding examples of serpentine neoendemics, that is, groups that evolved on ultramafics, rather than relicts or paleoendemic taxa secondarily restricted to serpentines (see Stebbins 1942; Kruckeberg 1954, 1984; Stebbins and Major 1965; Raven and Axelrod 1978; Mayer and Soltis 1994a, b).

Rarity. Discovery of *H. guggolziorum* along a paved, public road less than 3 miles from US Highway 101 at Hopland, near a University of California field station, probably reflects extreme rarity of the species and insufficient access by botanists to serpentines in the vicinity. Smith and Wheeler (1990–1991) explored some nearby ultramafic sites in Mendocino County and did not report any species referable to *Harmonia* in their flora of Mendocino County. I did not find collections of *H. guggolziorum* at CAS, CHSC, DAV, JEPS, PUA, ROPA, UC, or the herbarium of the University of California Hopland Research and Extension Center and am unaware of any collections of the species from anywhere other than the holotype and paratype localities. *Harmonia guggolziorum* is probably naturally rare, based on the paucity of documented localities for other serpentine harmonias; *H. doris-nilesiae, H. hallii,* and *H. stebbinsii* are all listed as rare or endangered (List 1B) by the California Native Plant Society (2001). Exploration for new populations of *H. guggolziorum* on ultramafics of southern Mendocino County and adjacent counties is needed.

I am pleased to name this species for Jack and Betty Guggolz of Cloverdale, California, who collected the first specimens of *Harmonia guggolziorum* and who have contributed significantly to conservation of California's North Coast Range flora through years of dedicated effort.

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A NEW SPECIES OF *DIDYMODON* (MUSCI) FROM CALIFORNIA

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ABSTRACT

A new moss species, *Didymodon eckeliae* R. H. Zander, is described from San Diego County in southern California. It is distinguished from its closest relatives in *Didymodon* sect. *Vineales* mainly by scalloped and bistratose leaf margins.

The Mediterranean climate of southern California supports an assemblage of arid-adapted mosses, of which *Didymodon* is a major element (Harthill et al. 1979; Koch 1950). A member of the harsh-environment family Pottiaceae (Zander 1993), *Didymodon* in North America and Mexico (Zander 1981, 1994, 1998) is composed of a number of complexes that are uncommonly difficult to identify to species with certainty. When a distinctive new species, as is here described, is discovered, it is a matter of amazement and gratification.

Didymodon eckeliae R. H. Zander, sp. nov.

Type: USA, California, San Diego Co., 13 km NE of Lakeside, Barona [Rancheria] Indian Reservation, trunk of *Quercus agrifolia,* I. L. Wiggins, April 9, 1954 (holotype, NY, segregated as "subpacket A"). Mixed with *Grimmia pulvinata* (Hedw.) Sm. & Sowerb.

Plantae in parte distali atrovirentes. Folia caulina mucronata, longi-lanceolata, in parte distali carinata, 2–3 mm longa, late crenata, in parte folii distali ⅔–¾ in margine bistratosa, cellulis eis laminae similibus praedita; costa brevi-excurrens e cellulis irregulariter subisodiametricis vel quadratis composita; cellulae basales foliares juxta costam subdistinctae, brevi-rectangulares, 11–14 μm latae, 1–3:1; parietes cellulares basales aeque incrassati vel tenues; sinus foliares crenulationum subfragiles. Lamina in KOH rubra reagens.

Plants growing in cushions, dark green above, tan below. Stems to 1.5 cm, branching often; rounded-pentagonal in transverse section, hyalodermis absent, sclerodermis weakly developed, diameter of central cylinder cells 20–25 μm, central strand present, strong; sparsely radiculose; axillary hairs 4–5 cells in length, basal cell thicker-walled or brownish. *Cauline leaves* incurved, appressed, somewhat twisted about the stem when dry, patent to spreading-recurved when moist; *long-lanceolate, adaxial surface keeled, 2–3 mm long;* base not differentiated or short-rectangular, sheathing; margins weakly recurved in proximal ⅓–½ of leaf, *evenly and broadly crenate and bordered by 1–2 rows of bistratose cells similar to the laminal cells in distal ⅔–¾ of leaf;* apex long-acuminate; *costa short-excurrent as a mucro of quadrate or irregular nearly isodiametric cells,* adaxial cells quadrate distal to leaf base, in 4 rows, abaxial cells quadrate distal to leaf base; transverse section semicircular, adaxial epidermis present, adaxial stereid band absent, guide cells 6 (4+2) in 2 layers, hydroid strand absent, abaxial stereid band present, lunate in cross section, abaxial epidermis present, weakly differentiated; *basal cells weakly differentiated at leaf base near the costa, short-rectangular, 11–14 μm wide, 1–3:1, walls of basal cells evenly thickened to thin-walled;* distal laminal cells quadrate-hexagonal, essentially homogeneous, 7–9 μm wide, 1:1, abaxial to adaxial wall width ratio 1:1, lamina 13–15 μm thick medially, thickness ratio of multistratose to unistratose portions of leaf 2:1, papillae multiplex, poorly defined, as thick, irregular caps over the lumens, cell walls evenly thickened, convex on both sides of lamina. Specialized asexual propagation: *leaf somewhat fragile at sinuses of crenulations.* Sexual condition: apparently dioicous, archegonia alone present, terminal on stem. Sporophyte unknown. *KOH laminal color reaction red.*

The new species is named for Patricia M. Eckel in gratitude.

This is the second new species of *Didymodon* Hedwig (Pottiaceae, Musci) to be discovered recently for California, USA (Zander 1999), though the present find is from taxonomically long-neglected herbarium material. It joins the species *D. norrisii* R. H. Zander and *D. nevadensis* R. H. Zander, from Nevada (Zander et al. 1995) as new western species of the genus. Two Asian species, *D. anserinocapitatus* (X.-j. Li) R. H. Zander (Zander and Weber 1997) and *D. tectorum* (Müll. Hal.) K. Saito (Zander and Ochyra 2001) have also been discovered in the American West. Given the acute and persistent activity of bryologists in California and elsewhere in the American West, it may confidently be predicted that additional new and exotic species of Pottiaceae, if not *Didymodon,* will detected.

The new species is reminiscent of *D. sinuosus* (Mitt.) Delogne of Europe in its broadly crenulate leaf margins (notches averaging about 8–10 cells apart), but that species has distinct teeth at the apex of at least the immature leaves, and the distal leaf margins are not bistratose or only rarely so in small
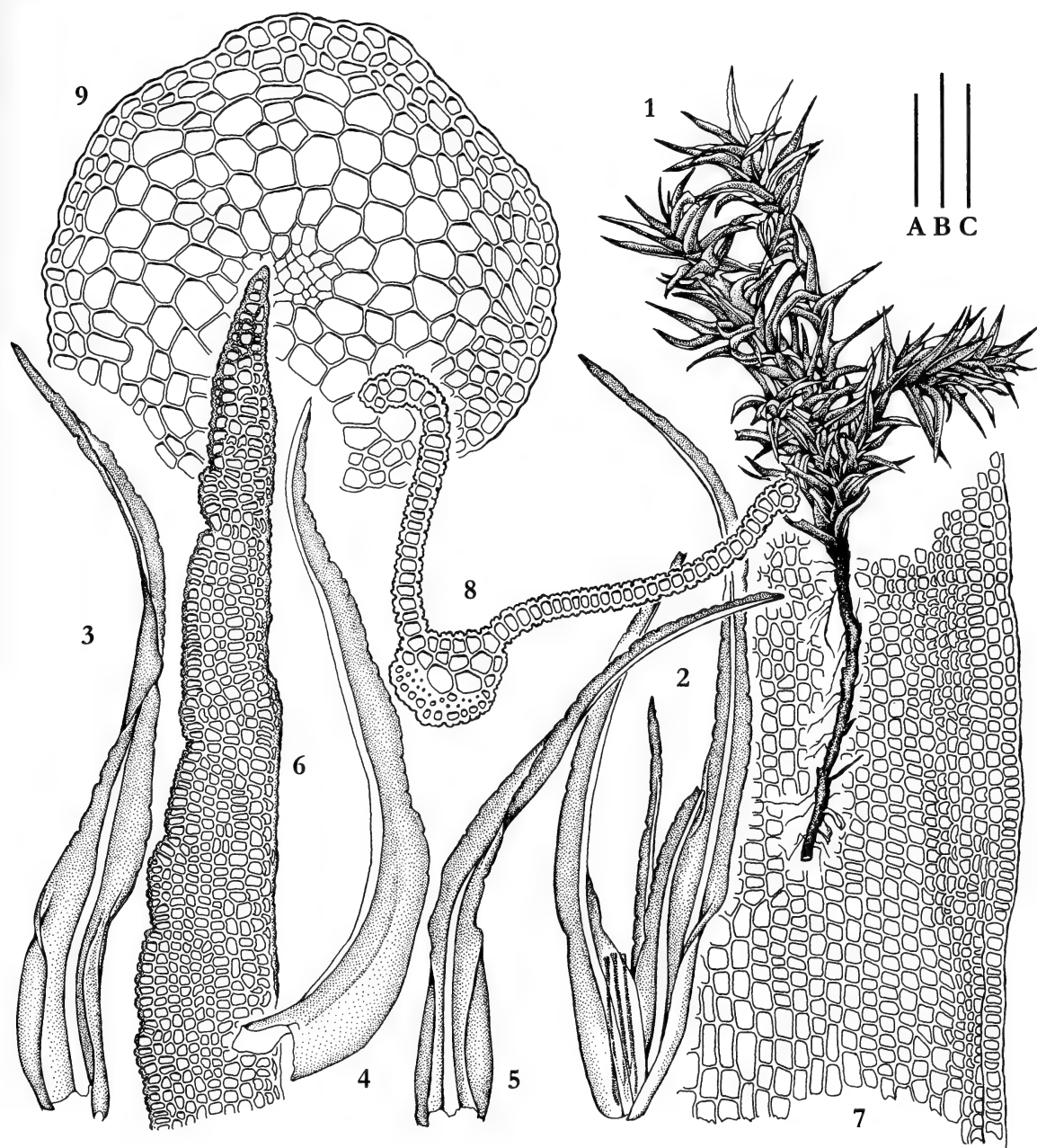
FIG. 1.   *Didymodon eckeliae.* 1. Habit. 2. Perichaetium. 3–5. Cauline leaves. 6. Leaf apex. 7. Leaf base. 8. Leaf cross section at mid-leaf. 9. Stem cross section. Scale bars: A = 4 mm (fig. 1); B = 0.5 mm (figs. 3–6); C = 70 μm (figs. 6–9).

patches. There are several moss species of the American Southwest and adjacent Mexico that have bistratose leaf margins that may be confused with the new species, but none have broadly crenulate (scalloped) leaf margins. It differs, additionally, from *D. rigidulus* var. *subulatus* (E. B. Bartram) R. H. Zander by the latter's long-subulate apex, and smooth leaf cells. *Didymodon australasiae* (Hook. & Grev.) R. H. Zander has a much flattened costal section. Species of the pottiaceous genus *Mironia*

R. H. Zander have strongly differentiated half-sheathing leaf bases. *Rhexophyllum subnigrum* (Mitt.) Hilp., likewise in the Pottiaceae, has deeply cleft leaf margins, but these are also dentate, and the distal portion of its leaves are bistratose in patches throughout.

The new species is closely related to *Didymodon vinealis* (Brid.) R. H. Zander, sharing such distinctive characters as weakly differentiated leaf base, transverse section of the costa at leaf base rather

concave, and the presence of a short, deep groove with the appearance of a long-elliptical window on the adaxial surface of the costa near the apex. This last distinctive feature is lacking in *D. sinuosus,* which, by its minutely crenulate leaf margins may be more closely related to *Trichostomum tenuirostre* (Hook. & Taylor) Lindb. It is similar to *D. nicholsonii* Culm. in many characters, but that also closely related species has broadly elliptical leaves with smooth margins and the costa is subpercurrent or percurrent. The common species *D. vinealis* is quite variable, and specimens with irregularly bistratose margins or unevenly notched leaves are not uncommon in California, but the combination, and regularity of the scalloping and evenness of the marginal band of bistratose cells is distinctive in the new species.

The original collection at NY was labeled only "*Trichostomopsis,*" a taxon presently recognized as *Didymodon* sect. *Asteriscium* (Müll. Hal.) R. H. Zander, probably because of the bistratose distal laminal margins and the lack of an adaxial costal stereid band. The new species, however, is immediately distinguished from species of that section by its weakly differentiated basal cells. The following key is based on that of Zander (1999).

KEY TO *DIDYMODON* SECT. *VINEALES* MORPHOLOGICALLY SIMILAR TO *D. ECKELIAE*

1. Leaves short- to long-lanceolate or long-triangular, to 4.0 mm, margins recurved near base or up to proximal ⅔ of leaf, propagula rare.
    2. Leaves unistratose or bistratose in very small patches marginally . . . . *Didymodon vinealis*
    2. Leaves bistratose marginally or medially.
        3. Leaves long-lanceolate, long-acuminate, margins evenly and broadly crenulate above leaf base, bistratose in 1–2 rows . . . .
        . . . . *Didymodon eckeliae*
        3. Leaves long-ovate to broadly lanceolate, apex blunt to broadly acute, margins smooth, bistratose marginally in 1–several rows in distal leaf half or occasionally only in patches . .
        . . . . *Didymodon nicholsonii*
1. Leaves deltoid to short-lanceolate or ovate, to 1.5 or rarely to 2.0 mm, margins recurved or revolute to near apex, propagula sometimes present.
    4. Costal section showing adaxial epidermal cells thin-walled, remainder of costa thick-walled; costa blunt apically, costa wider at midleaf than below, with a bulging adaxial surface forming a long-elliptic unistratose pad of cells, guide cells in 2(–3) layers, leaf margins loosely revolute, gemmae absent or at least rare, tubers occasional on proximal rhizoids . . . . *Didymodon nevadensis*

4. All cells of costal section about equally thickened; costa often with an apical conical cell or costa short-excurrent, costa gradually narrowing distally, adaxial surface usually nearly flat (but costa occasionally thickened and bulging adaxially), not forming a wide pad of cells, guide cells usually in 1 layer, leaf margins narrowly to loosely recurved, small spherical gemmae often present in leaf axils, rhizoidal tubers absent.
    5. Leaves ovate or ovate-lanceolate, 0.7–1.0 mm, base ovate or weakly differentiated, apex cucullate or weakly concave, margins weakly recurved, costa percurrent or very weakly excurrent from an obtuse or acute apex in 1–3 cells; lamina red in nature and with KOH, seldom green and KOH negative . . . . *Didymodon brachyphyllus*
    5. Leaves deltoid to deltoid-lanceolate, base squared, 1.0–1.5(–2.0) mm, apex flattened, or keeled, often somewhat reflexed, margins strongly recurved to revolute, costa excurrent from an obtuse apex as a several-celled blunt mucro; lamina green in nature and with KOH . . . . *Didymodon tectorum*

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REVIEW

Ecosystems of the World 16: Ecosystems of Disturbed Ground. Edited by Lawrence R. Walker. 1999. 868 pages. Elselvier Science Press, Amsterdam, The Netherlands.

For many years ecologists have examined the concept of ecological disturbance in relation to natural processes and community dynamics. Some have argued that much of what has been defined as disturbance is in fact an intrinsic part of natural systems. This book is a survey of contemporary topics relating to natural and anthropogenic disturbance, ecological succession, and environmental issues associated with disturbance. There are thirty-three individually authored chapters covering a broad range of interests. A general reading of the text gives the reader not only a sense of the variety of disturbance mechanisms, but also the range of approaches used to study them. The diversity of topics addressed in this volume makes this collection a valuable reference for researchers.

The editor suggests that the contributions be divided into the following categories: natural disturbance, anthropogenic disturbance, processes, and human response. After reading through the chapters it was difficult to delineate between those focusing on anthropogenic versus natural disturbance. Though some processes, such as volcanic and wind disturbance fall clearly under the heading natural disturbance, processes such as fire and erosion can be both natural and anthropogenic in origin. Interesting discussions on the categorization of disturbance as various types including natural and anthropogenic, endogenous and exogenous, and inherent and foreign could be found in many of the chapters.

Central issues such as the definition of the term disturbance in an ecological context are left up to each author resulting in an opportunity for a comparison of divergent views. Many authors cited well-established definitions. The most common of which were based on the "any relatively discreet event in time" concept put forth in the seminal work by Pickett and White "The Ecology of Natural Disturbance and Patch Dynamics." Other authors suggested their own definitions. Both I. K. Bradbury and L. R. Walker suggest definitions that included any process resulting in the loss of biomass. Several authors also suggested definitions based on new growth and colonization opportunities for individuals. An in-depth discussion of the use of the term disturbance can be found at the beginning of the chapter on disturbance in deserts authored by J. A. MacMahon. MacMahon suggests that the use of the "discrete event in time" definition does not adequately address extended climatic disturbances. The ambiguity of the term "disturbance," in relation to spatial and temporal scales, is also discussed by S. T. A. Pickett et al. in their chapter on patch dynamics.

The topics presented are generally discussed in sufficient detail. However, the rationale on how topics were selected for inclusion is unclear. Several chapters are dedicated to specific mechanisms of disturbance including glaciation, erosion, wind, volcanism, and mining. Other ecologically significant disturbance mechanisms such as fire and flood did not receive treatment in their own chapters. Similarly, several ecosystem types were discussed individually including deserts, boreal forests, Mediterranean shrublands, grasslands and savannas, North American wetlands, temperate forests, and urban areas, while others were omitted. A discussion of the criteria for selection in the introduction chapter would have improved an otherwise commendable work.

This book is useful as a tool for exploring divergent points of view on basic ecological questions. It has great value as a reference on a variety of subjects related to ecological disturbance, and would be useful as a supplementary text for students studying environmental issues and basic ecology.

—WILLIAM H. RUSSELL, USGS Western Ecological Research Center, Golden Gate Field Station. Fort Cronkhite Bldg 1063, Sausalito, CA 94965.

ANNOUNCEMENTS

New Editor

Beginning with Volume 49, the new editor for *Madroño* will be:

Dr. John Callaway
Department of Environmental Science
2130 Fulton Street
San Francisco, CA 94117-1080
email: callaway@usfca.edu

All new submissions should be sent to Dr. Callaway.

Donations in June McCaskill's Memory

The University of California at Davis is building a new herbarium facility, and the plant identification laboratory will be named for June. An exhibit of photos of June as well as information on her contributions to botany at UC Davis will be on display in the room. For more information, you can contact Ellen Dean at the UC Davis Herbarium

Contributions in June McCaskill's memory can be made to the UC Davis Foundation and sent to: Ellen Dean, Plant Biology, One Shields Ave., UC Davis, Davis, CA 95616.

PRESIDENT'S REPORT FOR VOLUME 48

Thanks to the tireless efforts of outgoing Editor Kristina Schierenbeck, I have the pleasure of providing this report for Volume 48 less than six months after my report for Volume 47. Yes, Kristina achieved her goal of bringing *Madroño* back onto publication schedule, to the great benefit of the California Botanical Society and to west American botany in general. Return to a normal publication schedule should have a positive effect on subscriptions, manuscript submissions, and article citations, in part by brightening the prospects for inclusion of *Madroño* in more on-line databases (in addition to BIOSIS). On behalf of the Society, I offer heartfelt thanks to Kristina for her hard work, dedication, and accomplishments. She now concludes her outstanding, extended service as Editor with *Madroño* in excellent health.

Our new Editor, John Callaway, is busily handling new submissions to *Madroño* (in coordination with Kristina Schierenbeck) and I am pleased to report that the transition between editorships is proceeding smoothly. John is an Assistant Professor of Environmental Science at the University of San Francisco, where he researches plant and soil ecology, especially in wetland systems. His role as a university instructor extends well outside San Francisco; John regularly visits Budapest, where he teaches in a Masters program in environmental management. The Society is indeed fortunate to have another conscientious, well-respected, and active scientist serving as Editor of *Madroño*. Many thanks to John for accepting this vitally important responsibility for the Society.

Attendance at our monthly meetings at UC Berkeley continues to rise, thanks in no small measure to First Vice-President Rodney Myatt, who once again organized an exciting lecture series for our program year. This fall, we have heard excellent presentations by Donald Strong, Richard Dodd, and Kevin Rice on research in the areas of plant ecology, evolution, genetics, and conservation biology. We are looking forward to lectures on diverse botanical topics by Bruce Mahall, Ron Amundson, Ingrid Parker, and John Callaway in winter and spring, 2002 (see www.calbotsoc.org). Thanks to Graduate Student Representative Kirsten Johannes, our monthly meetings have been more widely advertised than in past years and continue to be capped by lively post-lecture receptions in the University and Jepson Herbaria.

Second Vice-President Peter Fritsch is organizing the Society's annual banquet for 2002, which will be held at the U. C. Berkeley campus on 16 February. Our distinguished speaker for the occasion will be the world-renowned plant ecologist Chris Field, who will discuss his extensive research on the effects of global change on California ecosystems. The annual banquet is always a major highlight of our program year and promises to be especially enjoyable and educational in 2002, thanks to Peter Fritsch's efforts and Chris Field's participation.

The Council continues to pursue efforts to increase membership and visibility of the California Botanical Society and our journal, *Madroño*. A major challenge faced by the Council has been to find ways to promote timely membership renewals. Late renewals are much more welcome than lost memberships but do present financial and logistical difficulties for the Society (e.g., mailings of back issues). We can no longer afford to send *Madroño* to unrenewed members beyond the first issue of a new (unpaid) volume and I urge all members to respond as quickly as possible to renewal notices. We have begun offering regular members the option of renewing memberships for multiple years (at a discounted price) as a means of promoting continuity of memberships from year to year. Now that *Madroño* is back on publication schedule, we anticipate fewer late renewals.

Special thanks to Treasurer Roy Buck and Corresponding Secretary Sue Bainbridge for their dedicated hard work attending to the Society's membership services and financial concerns. Roy's and Sue's continual efforts are crucial to the Society and are responsible in part for our growing membership base. I also thank webmasters Curtis Clark and John LaDuke for recent improvements to our web site (www.calbotsoc.org), which no doubt will play an increasingly important role for the Society. Recording Secretary Dean Kelch and Council members Anne Bradley, Jim Shevock, and Bian Tan deserve thanks for their important contributions to planning and guiding the activities and future of the Society.

I welcome nearly 100 new members to the California Botanical Society and thank all members for your contributions and continuing support. I ask all of you to help us recruit new members and to encourage your library to continue or initiate subscription to *Madroño*. On behalf of the Council, I wish all of you a great year for botany in 2002!

—BRUCE G. BALDWIN
28 NOVEMBER 2001

EDITOR'S REPORT FOR VOLUME 48

This report serves to inform members of the California Botanical Society the status of *Madroño* from manuscripts submitted to papers published. Since the previous editor's report (see *Madroño* 47[4]) the journal received 62 manuscripts for review, including Articles, Notes, and Noteworthy Collections; 44 of these have been accepted for publication. The average time from article submission to publication has remained stable at approximately six months. Very few manuscripts were rejected after review. Authors of *Madroño* articles are generally quite responsive to reviewer and editorial suggestions.

There are many individuals who contribute to the editorial process; Jon Keeley, who continues to serve as book review editor; Steve Timbrook, who continues to assemble the Index and Table of Contents; Dieter Wilken and Margriet Wetherwax, who edit the Noteworthy Collections; Jeannie Trizzino, my editorial assistant; the Department of Biological Sciences at California State University Chico, that provides the funds to support Jeannie; Karen Ridgway at Allen Press; and members of the CBS executive council who enthusiastically support *Madroño* in every aspect. On behalf of the society, I thank the volunteer reviewers and the Board of Editors on whom we all depend to make the peer review process work for this valuable regional journal.

It has been a privilege to serve as editor of *Madroño* for four volumes, but I have passed the baton into the capable hands of Dr. John Callaway. Early indications give me the confidence that Dr. Callaway will keep a tight publication schedule and be devoted to the quality of the journal. I have appreciated the authors, reviewers, and readership who patiently overlooked my shortcomings and allowed me to grow into the position of editor. The editorial experience was a growth experience for me at many levels; I particularly enjoyed the opportunity to correspond with many colleagues with whom I might have not otherwise. Thank you, California Botanical Society, for the opportunity to serve the botanical community of western North America.

REVIEWERS OF *MADROÑO* MANUSCRIPTS 2001

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Barbara Wilson
Paul Wilson
Stephen Yool

INDEX TO VOLUME 48

Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

DEDICATION

June McCaskill

June McCaskill's career as the Curator of the UC Davis Herbaria spanned more than 37 years. She joined the Botany Department in 1953 and retired in 1991. June was born in Pasadena, California, in 1930, where her parents operated and owned a small nursery. Her father hybridized and sold camellias, naming one in honor of June; *Camellia japonica* 'June McCaskill.'

In 1951 June graduated from Mills College in Oakland with a degree in Botany. Soon after she began working for Professor Howard McMinn at Mills College, assisting in the small teaching herbarium and greenhouses. In 1953, she joined the herbarium at UC Davis.

At Davis, June established herself as one of the best taxonomist in the state, identifying thousand of specimens sent or brought in by faculty, Farm Advisors, land managers, students, and the general public. She was particularly good at identifying agricultural weeds and poisonous plants sent to her from the School of Veterinary Medicine at UC Davis. One of June's remarkable skills was her ability to identify plant fragments, including plant parts in hay bales, aquatic species left too long is sealed bags, and hairballs found in the throat of dead animals. She assisted in many criminal court cases, identifying seeds and plant fragments important to prosecutors.

During her tenure at Davis, June co-authored the *Growers' Weed Identification Handbook,* which is the most widely used weed guide in California. She was a founding member of the Friend of the Davis Arboretum, and even after her retirement in 1991 help to start the Davis Herbaria Society.

Over the years June won many awards for her accomplishments, including a two time recipient of the Outstanding Performance Award by the Botany Department at UC Davis, Award of Excellence presented by the California Weed Science Society, and the Award of Distinction by UC Davis. The latter award is the highest honor of the College of Agricultural and Environmental Sciences award at UC Davis. In 1988 she was selected for the Women in Botany Oral History Project at the Bancroft Library of UC Berkeley.

One of June's passions was to travel around the world examining plants and nature. In addition to her many trips throughout California, she organized and led expeditions to the mid-Atlantic states, Texas, Hawaii, Canada, Costa Rica, Norway, Sweden, New Zealand and Greece. On her trip to Greece, June collected and mounted approximately 2,500 specimens of historical significance.

To those many people who had the good fortune to know June, we will remember her humor, friendship, and unselfishness. June was a favorite among the many undergraduates she employed and the numerous graduate students she assisted. She had an uncanny way of correcting the mistakes of others without quenching their enthusiasm for using taxonomic keys. In her spirit and the enthusiasm and friendship she extended to everyone she met, we dedicate Madroño volume 48 to June McCaskill (1930–2001), botanist and friend.